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Efectos de la Intensificación Agraria sobre la Biodiversidad en agro-ecosistemas europeos.

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INTRODUCCIÓN GENERAL

La agricultura es el uso del suelo más extendido en la Unión Europea, con algo más de 170 millones de hectáreas (el 40 % de su superficie, Eurostat 2011) dedicadas a cultivos herbáceos y leñosos, y prados y pastizales permanentes. Estos aprovechamientos conforman hábitats abiertos, mantenidos artificialmente en etapas sucesionales tempranas, que alojan una gran parte de la biodiversidad europea (p.e. más del 50 % de las especies de aves, Sanderson et al. 2005). No obstante, es creciente la proporción de especies y poblaciones que presentan un estado de conservación desfavorable (para las aves, ver EBCC, 2011).

La riqueza biológica de los ambientes agrarios europeos no sólo se explica por la extensión que éstos ocupan actualmente, sino también por la persistencia a lo largo del Cuaternario de espacios más o menos abiertos (sin árboles o con un dosel arbóreo disperso), imbricados con otras zonas de dominio forestal en patrones más o menos complejos. Tanto en el norte y centro de Europa (Svenning 2002), como en el sur del continente (Suárez et al. 1992), este tipo de espacios persistieron ligados a enclaves con limitaciones naturales y fuertes perturbaciones (pobreza y salinidad edáficas, fuerte continentalidad, inundaciones, fuego o viento), mantenidos además por la acción de los grandes herbívoros silvestres (Vera 2000). Todo ello favoreció la adaptación y expansión de especies vegetales y animales ligadas a este tipo de hábitat abiertos, así como, en el sur, la dispersión de taxones de origen irano-turaniano y norteafricano, de carácter marcadamente estepario (Suárez et al. 1992). A medida que la presión humana fue reduciendo las poblaciones de herbívoros silvestres, el papel de éstos en el mantenimiento de los espacios abiertos fue sustituido a lo largo del

Neolítico por los herbívoros domesticados y los cultivos agrícolas. Así, la extensión de la "agricultura de primera generación" (Buckwell y Armstrong-Brown 2004) contribuyó a favorecer a especies vegetales y animales ligadas a este tipo de ambientes en expansión (Stoate 2011). Como resultado de todo ello, numerosas especies han evolucionado con la agricultura a medida que los sistemas agrarios han ido cambiando a lo largo del tiempo, de modo que los métodos más tradicionales o extensivos de agricultura son los que hoy en día contribuyen en mayor medida a la conservación biodiversidad local y global (Beaufoy et al. 1994).

A partir del siglo XVIII se inició una fase de creciente aplicación de energía y de tecnología a la producción agraria en muchas zonas del mundo, que culmina en el siglo XX con la denominada *Revolución Verde* (Hazell 2003). Las principales novedades que acompañaron a la "agricultura de segunda generación" tuvieron que ver con la mecanización de las prácticas agrarias, que posibilitaron y estimularon la aplicación de nuevas tecnologías en los ámbitos de la maquinaria, la biología, la química y en la transmisión de nformación en el medio agrario (Buckwell y Armstrong-Brown 2004). Acompañando estas novedades, y en el contexto de los cambios demográficos y sociales del mundo desarrollado, tuvieron también lugar drásticas modificaciones en los patrones de consumo de alimentos, así como un desarrollo masivo de las tecnologías aplicadas al transporte, almacenamiento, conservación, procesado y distribución de los mismos. Todo ello generó la capacidad y oportunidad para acometer operaciones de gran escala, intensivas en capital y altamente productivas, como drenajes, concentración parcelaria, regadíos, puesta en cultivo de tierras marginales, desarrollo de nuevas variedades y

razas, fertilizantes de síntesis y productos fitosanitarios, extensión de monocultivos, etc.

Todo este proceso de cambio en la agricultura, que se resume en el concepto de *intensificación agraria*, ha resultado en un incremento espectacular de los rendimientos en la mayor parte del mundo desarrollado, pero también en crecientes impactos ambientales, en particular sobre la biodiversidad, los paisajes agrarios y el funcionamiento de los ecosistemas (Matson et al. 1997, Donald 2004).

La intensificación agraria en Europa.

La Política Agraria Común (PAC) fue instaurada en 1962 con los objetivos de incremento de la productividad agraria, mejora de las rentas de los agricultores y garantía de alimentos a precios asequibles para los consumidores. La PAC se instrumentó homogéneamente en los sucesivos Estados Miembros, por medio de las *Organizaciones Comunes de Mercado*, ofreciendo subsidios a la producción y la exportación y regulando aranceles a la importación, y las *políticas estructurales*, apoyando económicamente la modernización de las explotaciones y las infraestructuras agrarias. Y se dotó de un ingente presupuesto económico que aún hoy consume alrededor del 40 % del presupuesto anual comunitario. Desde entonces, la PAC ha ido adaptándose al desarrollo de la agricultura europea y mundial, incorporando progresivamente objetivos de seguridad alimentaria, cohesión territorial, desarrollo rural y calidad de los alimentos, si bien sus mayores retos actuales son los ligados a la conservación de la biodiversidad y los paisajes y las comunidades rurales (Oñate 2005).

La homogénea aplicación de la PAC a las distintas realidades de los países europeos exacerbó las tendencias de cambio que estos venían experimentando en sus sectores agrarios, condicionados a su vez por sus diversas limitaciones edafo-climáticas y contrastadas estructuras y niveles de desarrollo (Potter 1997). La intensificación de las agriculturas europeas se desarrolló muy en conexión con los niveles de industrialización, centrándose en mayor medida en las zonas y actividades productivas donde más podían rentabilizarse los avances en los sectores industriales de la maquinaria, los fertilizantes, los plaguicidas y las semillas. Por ello, en comparación con los del centro y norte de Europa, los países mediterráneos, y en particular España, se incorporaron más tardíamente al proceso (Naredo 1986). Aun así, dentro de un mismo país los efectos de la modernización fueron, en general, menos acusados en las regiones con menor nivel de desarrollo y potencial agronómico, en las que persistieron métodos y prácticas de gestión más extensivas y dependientes de los recursos territoriales (en España por ejemplo las mesetas cerealistas, la ganadería de montaña y de dehesa, o las regiones olivareras). Por el contrario, las regiones con mayor potencial se incorporaron rápidamente a los modelos y prácticas de producción intensiva (p.e. en España, el litoral mediterráneo o el eje de las depresiones del Ebro o el Duero; Garrido y Moyano 1996). Como consecuencia de todo ello, existe una muy variada tipología de "agriculturas" a lo largo y ancho del continente, conviviendo incluso dentro de un mismo país realidades representativas de todo un gradiente entre las situaciones de marginalidad productiva y socio-económica, próximas al abandono, y la intensificación más acusada (Suárez et al. 1997). Las últimas

ampliaciones de la UE a los países del centro y este europeos no han hecho sino extremar estos gradientes.

En cualquier caso, si bien la intensidad del proceso de intensificación varía entre países y regiones, los cambios en los usos del suelo y las prácticas agrarias impulsados por la PAC son relativamente comunes (Pain y Dixon 1997) y pueden agruparse en tres dimensiones, atendiendo a la escala espacial a la que tienen lugar (Tivy 1990; Benton et al. 2003; Firbank et al. 2007):

- Cambios a nivel de parcela o campo de cultivo: uso más intensivo de la maquinaria agrícola, que faculta una gestión más precisa del cultivo; aumento de las dosis y frecuencia de uso de fertilizantes de síntesis y productos fitosanitarios, que promueve la uniformidad espacio-temporal en el establecimiento, crecimiento y maduración de los cultivos; mayores dosis de simiente que consiguen mayor densidad y uniformidad en las siembras; utilización de variedades de cultivo de alto rendimiento, que facultan una mayor productividad, y, como consecuencia de lo anterior, simplificación o desaparición de las rotaciones de cultivos, disminución o desaparición del barbecho y, eventualmente, transformación en regadío.
- Cambios a nivel de paisaje: simplificación y uniformización de los paisajes agrarios, como consecuencia tanto de la agregación de los cambios a nivel de parcela, como de las operaciones de concentración parcelaria y sus efectos de disminución de la densidad de linderos entre parcelas y de otros elementos no cultivados del paisaje (setos, eriales,

ribazos, bosquetes o bancales). Además, la consolidación de explotaciones en unidades de mayor tamaño para aprovechar economías de escala provoca una mayor continuidad espacial de áreas bajo los mismos sistemas de gestión y / o rotaciones de cultivos a lo largo del ciclo anual.

- Cambios a nivel regional: polarización del espacio, con grandes áreas contiguas dominadas por el mismo tipo de cultivo, en una agricultura especializada que reemplaza paisajes anteriormente caracterizados por sistemas de producción mixtos espacialmente entrelazados; y otras zonas menos productivas por limitaciones naturales afectadas por la disminución de la actividad o el abandono. En última instancia, la PAC y las dinámicas del desarrollo promueven diferentes tasas de intensificación o abandono entre regiones, comarcas y orientaciones productivas.

Los cambios en los componentes individuales de la intensificación se producen frecuentemente de modo correlacionado e incluso interdependiente, de modo que el cambio en un componente facilita el cambio en otros. La intensificación agraria resulta así en un proceso multifactorial que a lo largo de las últimas décadas ha modificado profundamente no solo la gestión de los cultivos a escala de parcela, sino también la estructura y funcionamiento de los agro-ecosistemas a escala de paisaje (Chamberlain et al. 2000). La dimensión paneuropea del proceso y la importancia de sus efectos hacen que la intensificación agraria sea considerada una amenaza global para la biodiversidad (Donald et al. 2001).

Efectos de la intensificación agraria sobre la biodiversidad europea.

La intensificación agraria es considerada responsable de los declives generalizados detectados en las especies de aves ligadas a los medios agrarios europeos, que desde la segunda mitad del siglo pasado han experimentado alarmantes descensos poblacionales no registrados en las especies asociadas a otros medios (p.e. Pain y Pienkowski 1997; Krebs et al. 1999; Sanderson et al. 2005; Donald et al. 2001; 2006). Por su alta detectabilidad, claridad taxonómica, nivel de conocimiento de su biología y su consideración general como buenos indicadores del estado de los ecosistemas (Gregory et al 2005), las aves han sido objeto de especial atención (EBCC, 2011), si bien se han detectado declives similares en otros grupos taxonómicos, como plantas (Marshall et al. 2003; Storkey 2006), organismos del suelo (Kladivko 2001), invertebrados (p.e. Aebischer 1991; Kromp 1999; Sunderland y Samu 2000; Weibull et al. 2000; Östman et al. 2001), y mamíferos (p.e. Harris y Woollard 1990).

En términos generales, esta pérdida extendida de biodiversidad, respondería, por un lado, a un aumento en la proporción de producción primaria apropiada por la agricultura y, por otro, a una disminución de la heterogeneidad ambiental en los sistemas agrarios. La optimización del cultivo resultante de su intensificación incrementa la proporción de producción primaria neta que es derivada al rendimiento agrario, de forma que disminuye la fracción disponible para la parte no cultivada del sistema, reduciendo, por ejemplo, las poblaciones de flora y fauna silvestre en los campos de cultivo (Haberl et al. 2004, Firbank et al. 2007). Por su parte, la intensificación a nivel de cada parcela tiene un

efecto agregado de simplificación y homogenización del paisaje agrario, resultando en una disminución de heterogeneidad ambiental a múltiples escalas que disminuye la diversidad de hábitats y nichos para las especies silvestres (Benton et al. 2003).

Como la intensificación agraria es, por tanto, un proceso multifactorial y multiescalar, la identificación de los componentes específicos más influyentes sobre la biodiversidad en un ámbito concreto resulta particularmente compleja (Stoate et al. 2001, Figura 1). En este sentido, se debate acerca de la preponderancia relativa que tienen los distintos factores y sus efectos agregados, que normalmente varía en función del grupo taxonómico observado (Firbank et al. 2007, Kleijn et al. 2011). La parcela individual se corresponde con la unidad de propiedad donde cristalizan las decisiones de gestión de cada agricultor, y en su caso, donde se detectan los efectos directos de las mismas sobre la biodiversidad. Pero el reconocimiento de que las especies interactúan entre sí y experimentan el paisaje circundante a diferentes escalas en función de sus capacidades dispersivas, ha puesto sobre la mesa la importancia de considerar el grado de complejidad del paisaje para entender las relaciones entre la biodiversidad y la agricultura. En este sentido, se ha resaltado la importancia del nivel paisajístico como dimensión de análisis para explicar la riqueza y abundancia de la biodiversidad y su dinámica en estos ambientes, así como la regulación y provisión de servicios ecosistémicos en los mismos (Bengtsson et al. 2003; Swiftet al. 2004; Tscharntke et al. 2005).

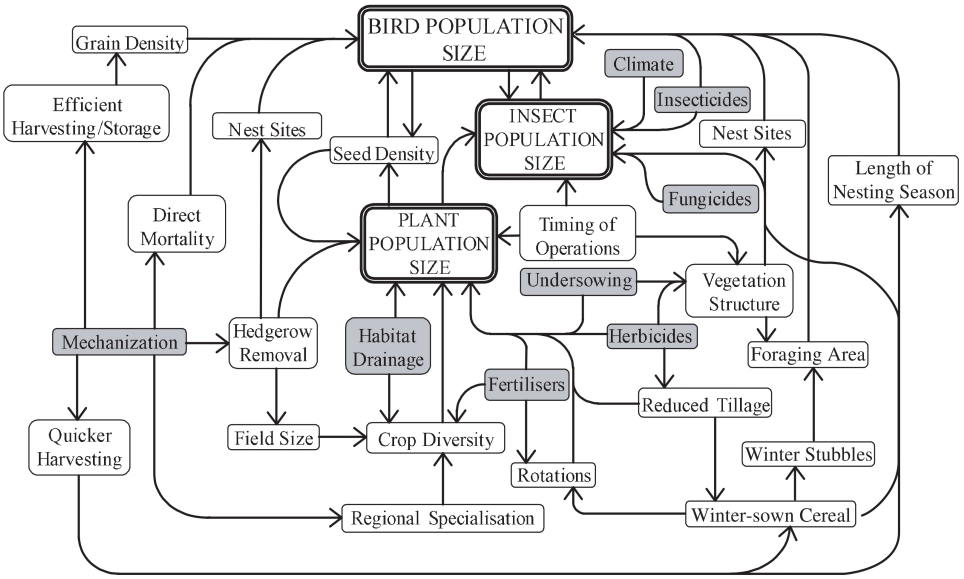

Figura 1. Causas potenciales de los cambios en las poblaciones de plantas, insectos y aves resultado de las modificaciones en las prácticas agrarias asociadas a la intensificación en Europa. (Robinson y Sutherland 2002).

La conservación de la biodiversidad en los sistemas agrarios europeos.

A partir de la década de los 90, la PAC comienza a incorporar la aplicación obligatoria y cofinanciada por cada Estado Miembro de *medidas agroambientales*. Se trata de incentivos económicos, de adopción plurianual y voluntaria por los agricultores, a cambio de la puesta en práctica de modalidades de gestión más compatibles con la conservación del medio ambiente y la biodiversidad. La responsabilidad en el diseño y gestión de las medidas corre a cargo de los Estados Miembros, tanto en lo que se refiere a la fijación de

objetivos concretos, como al establecimiento de los requisitos a cumplir por los agricultores que se acojan, de las primas compensatorias que van a recibir a cambio, y de los controles en campo para verificar el cumplimiento (Buller et al. 2000). El nivel de aplicación de las medidas agroambientales es creciente, alcanzando alrededor del 24 % de la superficie agraria UE-15 (unos 30,2 millones de ha), si bien muy desigualmente repartidas entre Estados Miembros (p.e. más del 75 % en Finlandia, Luxemburgo, Suecia y Austria y menos del 10 % en Grecia, España y los Países Bajos; datos de Eurostat).

Los estudios que han evaluado la efectividad de las medidas agroambientales orientadas a la conservación de la biodiversidad no son concluyentes. Así, algunas medidas parecen tener efectos positivos, mientras que otras no los tienen, e incluso los efectos de una misma medida pueden variar en función de la región en la que se aplique, o del grupo taxonómico estudiado (ver revisión en Kleijn y Sutherland 2006, Batáry et al. 2010). La capacidad de este instrumento para mejorar las condiciones de los sistemas agrarios en los que se aplican parece estar limitada por distintos aspectos, que van desde su naturaleza local, orientada a campos o explotaciones específicos (Wittingham 2007), hasta posibles diseños e implementaciones subóptimos (Llusia y Oñate 2005; Kleijn et al. 2006), pasando por el variable grado de acogida por parte de los agricultores que suelen experimentar. Un aspecto adicional a considerar tiene que ver con el tipo de efecto que se espera de las medidas, de *mejora*, donde esperaríamos cambios positivos en los indicadores analizados (p.e. riqueza o abundancia), o de *mantenimiento*, donde lo relevante es precisamente la ausencia de cambios negativos (Primdahl et al. 2003).

Además de las limitaciones de diseño y aplicación, la respuesta de la biodiversidad a estas medidas de conservación, estaría moderada también por la interferencia de distintos factores propios del agrosistema. A este respecto, se proponen dos hipótesis (ver Kleijn et al. 2011 y referencias allí):

- Efectividad moderada por la intensidad del uso: esta hipótesis se centra principalmente en procesos a nivel local, basándose en relaciones de competencia, y las teorías del nicho y la perturbación intermedia. Supone que la mayor heterogeneidad a nivel de parcela y la menor frecuencia de perturbaciones en los sistemas menos intensivos, facilita la existencia de comunidades más complejas a través de la provisión de una mayor estabilidad y diversidad de nichos. A medida que el sistema se intensifica, se produce una reducción de nichos disponibles, consecuencia de su homogeneización y el aumento en la frecuencia de perturbaciones. Debido a los efectos aditivos de los múltiples componentes de la intensificación, la biodiversidad disminuiría exponencialmente con la intensidad. Así, las medidas resultarían más efectivas en sistemas extensivos, sometidos a un manejo reducido y a un nivel medio de perturbaciones, donde el potencial incremento de biodiversidad provocado por el cambio en la intensidad de uso del suelo sería mayor para esfuerzos similares.
- Efectividad moderada por el paisaje: esta hipótesis otorga mayor importancia a la estructura del paisaje agrario, y se basa en las teorías de metapoblaciones (Levins 1969) y metacomunidades (Leibold et al. 2004). Así, la persistencia de

una población en un agrosistema dependería de continuos procesos de colonización y extinción, tanto en hábitats cultivados como no cultivados. En un paisaje simple, donde predominan los campos de cultivo y los parches semi-naturales están aislados, la extinción sería el proceso dominante, con la consiguiente pérdida de biodiversidad. En un paisaje complejo, sin embargo, un mosaico de hábitats diversos equilibraría las tasas de colonización y extinción. Esta hipótesis predice que la efectividad de las iniciativas de conservación es mayor en paisajes relativamente simples (de 2 % a 20 % de hábitats semi-naturales en la matriz), ya que las fuentes de colonización están presentes y la biodiversidad en la matriz cultivada no está mantenida por una constante aportación de especies desde los elementos no cultivados circundantes, como ocurre en los paisajes complejos.

La falta de consenso sobre las causas de la efectividad variable de los esfuerzos por revertir la pérdida de biodiversidad, evidencia la necesidad de seguir investigando cómo las prácticas agrarias actuales afectan a las comunidades biológicas, con el fin de apoyar el diseño de medidas de conservación efectivas. Así mismo, la naturaleza de las herramientas de conservación disponibles, que implican la participación necesaria de diversos agentes (administraciones, agricultores...) requiere la identificación de los factores ligados a las prácticas agrarias más relevantes, sobre los que actuar a través de medidas aplicables y eficaces.

OBJETIVOS Y ESTRUCTURA DE LA TESIS

Con el fin de contribuir al desarrollo de medidas de conservación efectivas, el objetivo principal de esta Tesis es analizar las relaciones entre los componentes de la intensificación agraria y la variación en la estructura y composición de las comunidades biológicas de los agro-ecosistemas cerealistas europeos, tanto a nivel local (de campo de cultivo), como a nivel de los efectos agregados que las prácticas agrarias tienen en el paisaje, procurando identificar los efectos concretos de factores particulares de gestión de los sistemas agrícolas sobre estas comunidades.

A tal fin, se analizan los efectos de prácticas agrarias habituales a nivel de campo de cultivo, así como de la estructura y composición del paisaje circundante sobre las siguientes características biológicas de las comunidades biológicas de los sistemas agrarios:

1. Riqueza y composición taxonómicas.

En el Capítulo I, se analiza la variación de la riqueza taxonómica de plantas arvenses, coleópteros carábidos y aves especialistas de medios agrarios, en un sistema cerealista mediterráneo, en relación con la intensidad de uso del suelo agrícola. Se trata de identificar los factores con mayor influencia sobre la riqueza específica observada de estos tres grupos.

En el Capítulo II, se evalúa el efecto relativo de la intensificación agraria y la localización geográfica sobre la variación de la composición y abundancia de especies en las comunidades de aves especialistas de medios agrarios a lo largo de un gradiente geográfico que incluye ocho zonas de estudio europeas, procurando identificar los

factores de intensificación agraria con mayor influencia sobre estas características estructurales.

2. Abundancia.

En el Capítulo III, se analiza, en seis países europeos, el impacto específico de dos grupos de factores de intensificación agraria sobre la densidad de individuos y territorios de aves especialistas de agro-ecosistemas cerealistas: un grupo de factores relacionados con la gestión agraria a nivel del campo de cultivo y un grupo de factores relacionados con la modificación de la estructura y composición del paisaje circundante. Se examina también la contribución de cada factor en particular, dentro de estos grupos, a la explicación de la variación en la densidad de estas aves ligadas a medios agrarios. Este mismo análisis se aplica al caso concreto de la especie *Alauda arvensis* (Alondra común).

3. Estructura funcional.

En el Capítulo II, se evalúa la influencia de factores concretos de intensificación agraria sobre la estructura funcional de las comunidades de aves especialistas de medios agrarios a lo largo de un gradiente geográfico que incluye ocho zonas de estudio europeas, analizando la respuesta de distintas medidas de la diversidad funcional de las comunidades de aves a estos factores.

En el Capítulo V, se analiza en un sistema cerealista mediterráneo la respuesta de la diversidad funcional de la comunidad de plantas arvenses a dos gradientes independientes de intensificación agraria: un gradiente de intensidad de uso del suelo a escala de campo de cultivo,

y un gradiente de estructura y composición a escala de paisaje. Se analiza, así mismo, cómo varía la relación entre esta diversidad funcional y la riqueza taxonómica de la comunidad a lo largo de estos gradientes.

4. Relaciones interespecíficas dentro de la comunidad.

En el Capítulo IV, se estudia el patrón de asociación espacial interespecífica de territorios en un ensamblado de especies de aves paseriformes en un sistema cerealista mediterráneo, considerando la influencia tanto en el patrón de asociación, como en la abundancia particular de tres de las especies consideradas en la comunidad (*Miliaria calandra* Triguero *Galerida cristata* Cogujada común y *Cisticola juncidis* Buitrón) de diversos factores de intensificación agraria.

CONTEXTO DE LA TESIS Y METODOLOGÍA GENERAL

Contexto de la Tesis.

Esta Tesis se ha realizado en el marco del proyecto AGRIPOPES (*AGRIcultural Policy-Induced landscaPe changes: effects on biodiversity and Ecosystem Services*) dentro del programa EuroDiversity de la Fundación Europea para la Ciencia (European Science Foundation, ESF). Durante los años 2006-2009, un consorcio de onceocho equipos de investigación de diez países europeos estudió el efecto de la intensificación agraria sobre la diversidad biológica de los agro-ecosistemas cerealistas europeos y algunos de los servicios ecosistémicos que ésta proporciona.

Entre los principales objetivos de este proyecto, se encontraba la evaluación a escala europea de los cambios en la biodiversidad, la simplificación de redes tróficas y el potencial de control biológico de plagas agrícolas en los agro-ecosistemas causados por la intensificación agraria, mediante el uso de métodos y protocolos estandarizados comunes a todos los equipos de investigación implicados.

Áreas de estudio.

Los estudios que componen esta Tesis se desarrollaron en dos ámbitos geográficos: los capítulos I, IV y V se localizaron en un área de cultivo cerealista en el centro de España y los capítulos II y III abarcan un conjunto de ocho zonas de estudio en siete países europeos, que incluye la mencionada área española. (Figura 1).

Figura 1. Localización de las 8 zonas muestreadas en 7 países europeos comprendidas en los estudios de esta Tesis: 1. España (SP), 2. Irlanda (IR), 3. Holanda (NT), 4. Alemania (Jena, EG), 5. Alemania (Göttingen, WG), 6. Suecia (SW), 7. Polonia (PO), 8. Estonia (ES).

Se trata en todos los casos de regiones agrícolas donde domina el cultivo de cereal de invierno y que representan un doble gradiente geográfico/bioclimático y de intensificación agraria a escala europea. A continuación, y a efectos ilustrativos, se muestran en las figuras 2 y 3, los valores promedio de algunas de las variables de intensificación agraria utilizadas en el marco de este proyecto, tanto a nivel de campo de cultivo y de explotación, como de composición y estructura del paisaje alrededor de los puntos de muestreo (ver descripción detallada de las variables y listado exhaustivo más adelante). Como puede verse, las regiones más intensificadas en cuanto a la aplicación de insumos a escala local (Figura 2) son el área de estudio irlandesa y el área de

estudio de Jena (antigua Alemania Oriental), mientras que es en el área de estudio española donde menor cantidad de insumos se aplican. Precisamente, la menor cantidad de aplicaciones de fertilizantes y pesticidas a nivel de campo de cultivo se corresponde con una mayor intensidad de otras prácticas, como el control mecánico de plantas arvenses o la densidad de simiente sembrada Entre los valores más altos de esta última variable se encuentran regiones como la española, la polaca o la estonia (Figura 2).

En cuanto a las variables de composición y estructura tanto a nivel de explotación, como a escala de paisaje alrededor de los campos muestreados, las zonas de estudio de Jena y Estonia presentan los mayores tamaños de explotación y de campos de cultivo (Figura 3). Junto con las áreas holandesa y polaca, presentan también los porcentajes más altos de cobertura de tierra arable, a la vez que las mayores diversidades de cultivos (Figura 3). Precisamente, el área polaca, junto con las áreas de estudio española e irlandesa presentan los campos de menor tamaño. Los paisajes en las regiones española e irlandesa son los que presentan un menor porcentaje de cobertura de tierra arable, y es precisamente el área de estudio española la que presenta la diversidad de cultivos más baja en toda la muestra (Figura 3).

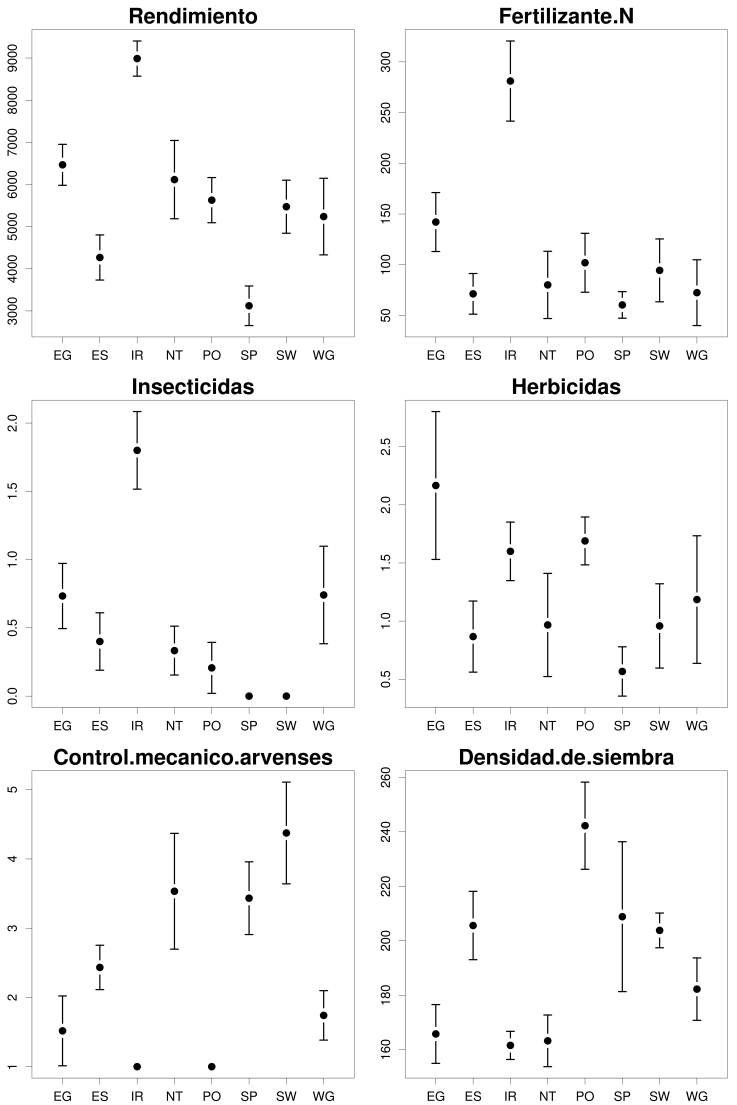

Figura 2. Diferencias entre las ocho zonas de estudio europeas en los valores promedio de variables de intensidad de uso del suelo a escala de campo de cultivo. Las barras de error indican los intervalos de confianza al 95 % . Alemania (Jena, EG), Estonia (ES), Irlanda (IR), Holanda (NT), Polonia (PO), España (SP), Suecia (SW), Alemania (Göttingen, WG).

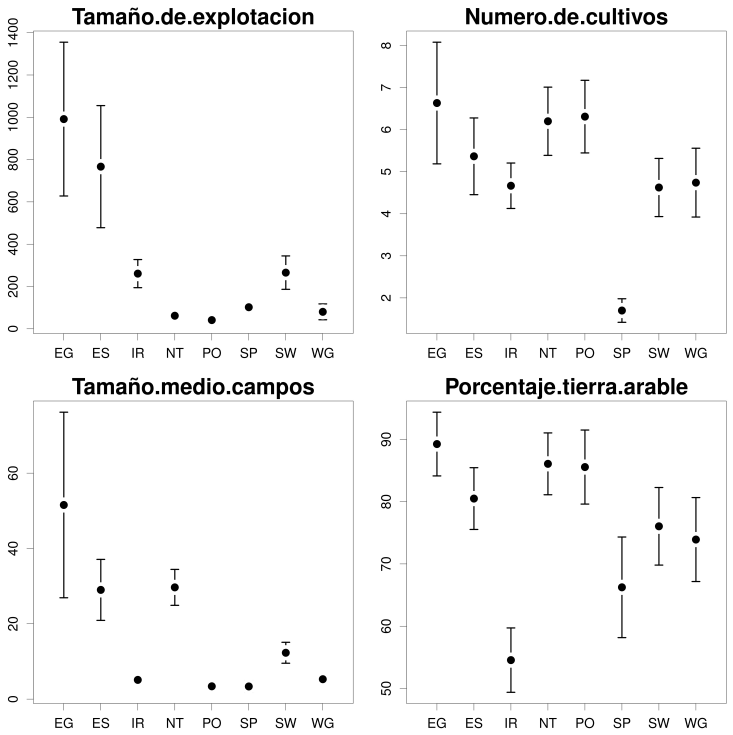

Figura 3. Diferencias entre las ocho zonas de estudio europeas en los valores promedio de variables de estructura y composición a escala de explotación y paisaje. Las barras de error indican los intervalos de confianza al 95 % . Alemania (Jena, EG), Estonia (ES), Irlanda (IR), Holanda (NT), Polonia (PO), España (SP), Suecia (SW), Alemania (Göttingen, WG).

El área de estudio española en la que se localizaron los trabajos descritos en los capítulos I, IV y V (incluida también en los capítulos II y III) es un ámbito de poco relieve en el centro de España (40º 40' N, 3º 25' W, Figura 4). La temperatura media anual es de 14,1 ºC de veranos calurosos (media de temperaturas máximas 33 ºC) e inviernos suaves (media de temperaturas mínimas 0,3 ºC) y la media de precipitaciones anual es de 400 mm, concentrados principalmente durante el verano y el otoño (AEMET 2008). Como en otras zonas

cerealistas similares del centro de la península Ibérica, las prácticas agrarias tradicionales han resultado en un mosaico agrario dinámico, con campos de diverso tamaño (en un rango de 0,5-30 ha) y un desarrollo variable de lindes, principalmente herbáceas. El paisaje está dominado por cultivos de trigo y cebada de invierno, así como barbechos anuales, resultado de rotaciones de cereal de año y vez, que cubren el 86 % del territorio. El resto del área está ocupada por barbechos de más de dos años, matorrales de transición y, marginalmente, cultivos leñosos (0,6 % del área total). El rendimiento medio en el área de estudio está alrededor de 3000 kg/ha, dentro del rango medio de las regiones de cultivo en secano de España (media ± SD, 3256±710 kg/ha; MARM, 2008), pero considerado como un sistema de baja intensificación en el contexto europeo (Bignal y McCracken, 1996). Debido a las importantes poblaciones de aves esteparias que alberga, el área de estudio está parcialmente incluida en la Zona de Especial Protección para las Aves (ZEPA) "Estepas cerealistas de los ríos Jarama y Henares" (código ES0000139), y en la Zona Especial de Conservación (ZEC) "Cuencas de los ríos Jarama y Henares" (código ES3110001). designados bajo las Directivas Aves y Hábitat de la Unión Europea. En noviembre de 2011, con posterioridad a la realización de nuestros estudios, fue aprobado el Plan de Gestión de estos espacios.

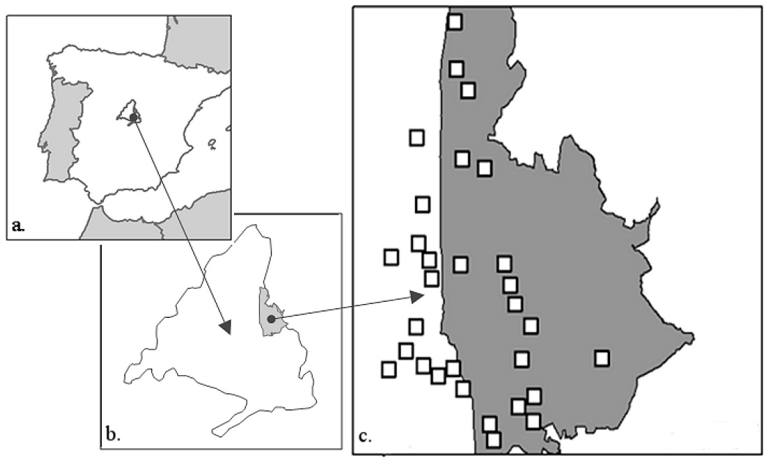

Figura 4. Localización del área de estudio en el centro de España. El ámbito incluido en la ZEPA y la ZEC aparece sombreado en b. y c. Las explotaciones seleccionadas en el área de estudio se muestran en c.

Metodología general.

A continuación se describen los procedimientos comunes diseñados para el proyecto AGRIPOPES, de acuerdo con los cuales se han obtenidos los datos analizados en los distintos capítulos que componen esta Tesis.

Selección de explotaciones y campos de cultivo.

Dada la diversidad de estructuras agrarias existente en los distintos países participantes en el proyecto, en el marco de AGRIPOPES, se considera una explotación agrícola (*ecological farm unit*) como:

- un conjunto de uno o más campos de cultivo, separados por una distancia no superior a 1km.
- estos campos son cultivados por el mismo agricultor, en propiedad o arrendados.
- cada explotación ocupa un área no superior a 1 km^2.

En cada zona de muestreo (una por país, salvo en el caso de Alemania, donde se establecieron dos áreas de estudio, ver más abajo) se seleccionaron 30 explotaciones, separadas por al menos un km de distancia, y que fueran representativas de un gradiente de intensificación agraria regional. Estas explotaciones se encontraban en regiones de entre 30x30 km^2 y 50x50 km^2 con el fin de limitar la β-diversidad y evitar la heterogeneidad de paisajes y tipos de suelo dentro de cada zona de estudio. En las explotaciones seleccionadas (de agricultura convencional o ecológica) se cultivó, durante el año de muestreo, cereal, mayoritariamente trigo de invierno (80 %,) y en ningún caso se muestrearon campos con otros tipos de cultivos en una misma explotación. Los campos muestreados nunca fueron menores de 1 ha, ni irrigados. El indicador para determinar el gradiente de intensificación regional fue el rendimiento promedio de cereal en los tres años anteriores al muestreo, que se llevó a cabo en 2007. Las explotaciones se seleccionaron de forma que el rango de productividad de cereal fuera el máximo posible, con una distribución homogénea..

Seleccion de puntos y muestreos de biodiversidad.

Para los muestreos de biodiversidad, se seleccionaron cinco puntos de muestreo en cada explotación. En cada uno de ellos se muestrearon plantas arvenses e invertebrados epigeos mediante la colocación de tres unidades muestrales (*plots*) de vegetación y dos trampas *pitfall* para invertebrados. Los puntos de muestreo se localizaron, siempre que fue posible, en cinco campos distintos (de una misma explotación) de trigo de invierno. Cuando hubo menos de cinco campos disponibles, los puntos se estratificaron de forma proporcional al tamaño de los campos muestreados. Los puntos de muestreo se

situaron paralelos a una linde herbácea (no leñosa) de la que se separaron 10 m hacia el centro del campo. Cuando se colocó más de un punto en un mismo campo de cultivo, éstos se separaron al menos 50 m, procurando siempre que esa distancia fuera máxima (Figura 5).

Las plantas se muestrearon en tres unidades (*plots*) de 2x2 m^2 paralelos al borde del campo y separados entre ellos por una distancia de cinco metros (Figura 5). En cada unidad se recogió información de presencia y abundancia de todas las especies presentes. Los muestreos se realizaron una vez durante el periodo de antesis del trigo.

Los invertebrados epigeos se muestrearon usando dos trampas *pitfall* por punto de muestreo situadas en el centro de las unidades de vegetación más extremos (Figura 5). Las trampas se protegieron con una cubierta plástica para evitar el efecto de las precipitaciones y posibles predadores, y se rellenaron con 150 ml de etilenglicol al 50 %. La determinación se limitó a los coleópteros de la familia de los carábidos y se llevó a cabo sólo en una de las dos trampas de cada punto y periodo de muestreo. La identificación se realizó a nivel de especie y se contabilizaron todos los individuos (el trabajo de determinación se encargó, en todos los casos, a los mismos expertos del Instituto de Ecología de Ceske Budejovice, República Checa). Las trampas se mantuvieron abiertas durante 7 días consecutivos en dos periodos: una semana después del comienzo del espigado del trigo, y otra al comienzo del estado lechoso del grano.

Dadas sus características de movilidad, el muestreo de aves se realizó sobre un área mayor: se muestrearon en cuadrados de 500x500 m^2 centrados en el mayor campo muestreado de cada explotación (Figura 5), de forma que sólo se muestreó un área de aves para cada

explotación. El método utilizado para los censos de aves fue una versión simplificada de Censo de Aves Comunes del *British Trust for Ornithology* (BTO, Bibby et al. 1992). El muestreo total consistió en tres visitas, en intervalos de tres semanas, durante la primavera y el verano de 2007. Las visitas comenzaron de acuerdo al calendario fenológico local de cada zona de estudio. Se censaron los individuos de todas aquellas especies que mostraron algún tipo de acción relacionada con el cuadrado de muestreo. La asignación de las especies de aves a la categoría de especialistas de medios agrarios se realizó mediante criterio experto para cada una de las zonas de estudio. La confirmación de territorios de cría de estas especies se hizo utilizando las tres visitas de censo y aplicando los siguientes tres criterios, dependiendo de la detectabilidad y el comportamiento reproductor de estas aves especialistas (Tabla 1):

- Para confirmar un territorio de cría de las especies de categoría A (especies de fácil detección, presentes durante toda la primavera), se precisaba su detección por lo menos en dos visitas mostrando comportamiento territorial (canto, llamada, defensa de territorio...) en la misma localización.
- En la categoría B se incluyeron especies que difícilmente aparecerían durante las tres visitas (p.e. migradoras de largo recorrido y estrictamente estivales) y especies consideradas de difícil detección. Para esta categoría sólo se requirió una observación mostrando comportamiento territorial.
- Para las especies de categoría C, se requirió evidencia directa de actividades reproductoras para confirmar un territorio de cría en el cuadrado de muestreo.

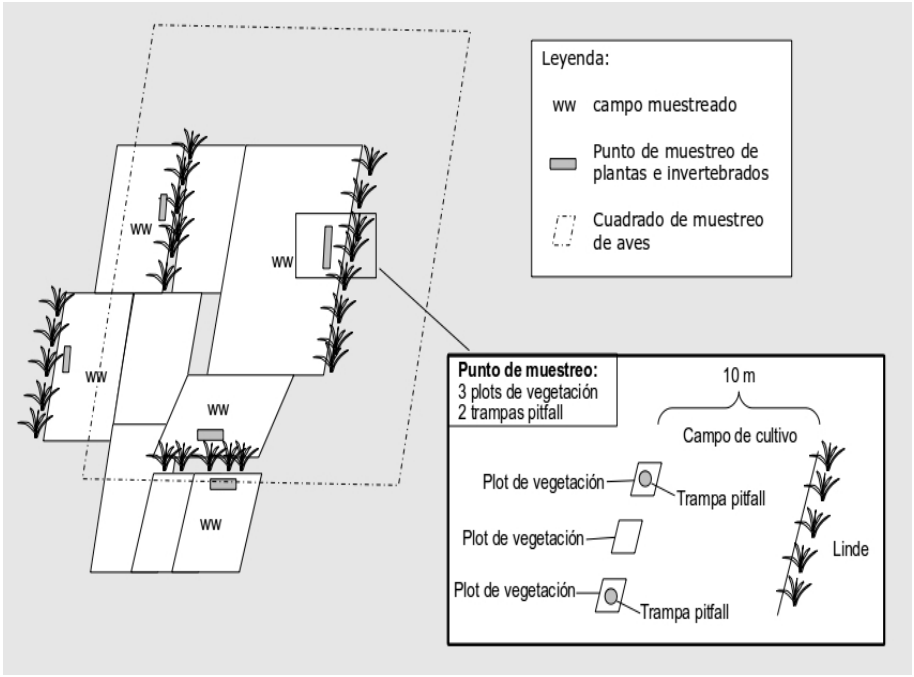

Figura 5. Disposición esquemática de puntos de muestreo de invertebrados y plantas y de cuadrados de muestreo de aves en una explotación agraria.

Tabla 1. Listado de las especies de aves consideradas especialistas de medios agrarios en el marco del proyecto AGRIPOPES incluidas en esta Tesis. Siglas BTO: siglas del nombre de la especie en inglés según *British Trust for Ornithology*. Categoría territorial: categoría adjudicada para la confirmación de los territorios de cría.

Nombre científico	Nombre común	Siglas BTO	Categoría territorial
Acrocephalus palustris	Carricero políglota	MW	B
Alauda arvensis	Alondra Común	S.	A
Alectoris rufa	Perdiz roja	RL	B
Anas platyrhynchos	Ánade real	MA	C
Anas strepera	Ánade friso	GA	C
Anser anser	Ánsar común	GJ	C
Anthus campestris	Bisbita campestre	TPI	B
Anthus pratensis	Bisbita común	MP	A
Burhinus oedicnemus	Alcaraván común	TN	A
Calandrella brachydactyla	Terrera común	STL	A
Circus aeruginosus	Aguilucho lagunero	MR	C
Circus cyaneus	Aguilucho pálido	HH	C
Circus pygargus	Aguilucho cenizo	MO	C
Cisticola juncidis	Buitrón	FTW	A
Coturnix coturnix	Codorniz común	Q.	B
Crex crex	Guión de codornices	CE	B
Emberiza citrinella	Escribano cerillo	Y.	A
Emberiza hortulana	Escribano hortelano	OBU	B
Galerida cristata	Cogujada común	CLA	A
Gallinago gallinago	Agachadiza común	SN	A
Haematopus ostralegus	Ostrero euroasiático	OC	A
Limosa limosa	Aguja colinegra	BW	A
Lullula arborea	Totovía	WL	A
Melanocorypha calandra	Calandria común	CAL	A
Miliaria calandra	Triguero	CB	A
Motacilla flava	Lavandera bollera	YW	A
Numenius arquata	Zarapito real	CU	B
Oenanthe oenanthe	Collalba gris	W.	A
Otis tarda	Avutarda común	GBU	B
Perdix perdix	Perdiz pardilla	P.	B
Phasianus colchicus	Faisán común	PH	A
Saxicola rubetra	Tarabilla norteña	WC	A
Saxicola torquata	Tarabilla común	SC	A
Tetrax tetrax	Sisón común	LBU	B
Vanellus vanellus	Avefría	L.	A

Medidas de intensificación agraria.

Las variables de intensificación agraria a escala de campo de cultivo y explotación, se obtuvieron a través de cuestionarios realizados en entrevista personal a todos los agricultores propietarios de los campos o encargados de su gestión, y con el apoyo de mapas digitales procesados en un Sistema de Información Geográfica (Tablas 2 y 3).

Se obtuvieron cuatro variables de estructura y composición de paisaje con la herramienta de AcrView Patch Analyst 3.12 (Rempel et al., 1999) en círculos de radio de 500 m alrededor de cada punto de muestreo y coincidiendo con el centro del cuadrado de 500x500 m^2 de muestreo de aves:

- Tamaño medio de parcelas de tierras arables en el radio.
- Desviación estándar del tamaño medio de parcelas de tierras arables en el radio.
- Porcentaje de superficie ocupada por tierras arables en el radio.
- Índice de Shannon de diversidad de usos del suelo en el radio, basado en las siguientes categorías, de acuerdo con las definiciones del *European Topic Centre on Land Use and Spatial Information* (Büttner, Feranec y Jaffrain 2000):
  - Superficies urbanas continuas.
  - Superficies urbanas discontinuas.
  - Tierras arables cultivadas.
  - Barbechos incluidos en sistemas de rotación.
  - Cultivos permanentes.
  - Bosques.
  - Matorrales de transición.
  - Masas y cursos de agua.

Tabla 2. Información a escala de explotación, recogida para cada una de las explotaciones seleccionadas**.**

	Medida	**Unidad**	**Comentarios**
Características físicas	Tamaño de explotación	ha	Total de superficie agraria útil propiedad/arrendada por un agricultor "*economical farm unit*"
	Área cultivada	%	
	Área no cultivada	%	
	Área construida-pavimentada	%	
	Área con medidas agro-ambientales	%, tipo y duración	Medidas agro-ambientales, cultivo ecológico, integrado, etc.
Cultivo	Número y tipo de cultivos en la explotación		Durante el año agrícola de muestreo 2006/07

Tabla 3. Información a escala de campo, recogida para cada uno de los campos muestreados.

	Variable	Unidad	Comentarios
Puntos de muestreo	Coordenadas espaciales	°, ‘, “, N,E,W	
Características físicas	Tamaño de campo	ha	
	Forma (ratio perimetro/area)	m^{-1}	
	Orientación	Grados	
	Pendiente	%	
	Altitud	msnm	
	max.% de área inundada		Durante el invierno 2006/07
	Tipo de suelo		
Cultivo	Sistema de rotación		Cultivos y orden de cultivos
	Densidad de siembra	# semillas/m^2	
	Roturado	cm, num. de operaciones, época	Profundidad, frecuencia, fecha
	Control mecánico de arvenses	Num. de aplicaciones, época	Tipo, frecuencia, fecha
	Cultivos fijadores de N previos al cereal	S/N	Tipo
	Variedad de cereal		
Rendimiento	Rendimiento	kg/ha en 2007	Basado en humedad de grano estandarizada (16 %)
Insumos	Fungicidas	Num. de aplicaciones, kg/ha, época	Marca comercial, cantidad, fecha de aplicación
	Insecticidas	Num. de aplicaciones, kg/ha, época	Marca comercial, cantidad, fecha de aplicación
	Herbicidas	Num. de aplicaciones, kg/ha, época	Marca comercial, cantidad, fecha de aplicación
	Tratamiento de semillas	S/N	Marca comercial, tipo, fecha
	Aplicación de N, P, K	kg N, P, K/ha,época	Cantidad, fecha
	Fertilizantes orgánicos	Si/no, kg/ha, época	Tipo, contenido en N, fecha de aplicación




CAPÍTULO I

Influencia de las prácticas agrarias sobre la riqueza de plantas arvenses, coleópteros carábidos y aves en un sistema cerealista mediterráneo.

Este capítulo reproduce íntegro el siguiente manuscrito:
Guerrero,I.; Martinez,P.; Morales,M.B. & Oñate,J.J. (2010) Influence of agricultural factors on weed, carabid and bird richness in a Mediterranean cereal cropping system. Agriculture, Ecosystems and Environment, 138: 103-108

Resumen

Mediante una metodología de inferencia basada en múltiples modelos, en este artículo, se identifican e interpretan los factores, a nivel local y de contexto paisajístico, más relevantes a la hora de explicar variabilidad en la riqueza de aves, coleóperos carábidos y plantas arvenses en un sistema cerealista de baja intensificación agraria en el centro de España. La riqueza de plantas arvenses se asoció negativamente con la densidad de simiente sembrada, la aplicación de herbicidas y el tamaño medio de los campos alrededor de los puntos muestreados. La riqueza de especies de carábidos se realcionó negativamente con la fertilización con Nitrógeno pero positivamente con la diversidad de coberturas del suelo alrededor de los puntos muestreados y el Fósforo aplicado. La riqueza de especies de aves se vio influenciada positivamente por el tamaño del campo muestreado, pero negativamente por la diversidad de coberturas del suelo en el paisaje circundante, la densidad de simiente sembrada, y la aplicación de Potasio. A pesar de que los tres grupos biológicos reflejaron la influencia de factores de intensificación agraria operando a distintas escalas espaciales, los factores más relevantes fueron específicos para cada grupo en particular. Estos resultados son relevantes para la selección de objetivos de medidas agro-ambientales orientadas a revertir el impacto de la intensificación agraria en la biodiversidad.

Abstract

Using a multimodel inference approach, the most relevant field-level and landscape context factors explaining the simultaneous variability of bird, carabid and weed species richness were identified and interpreted in a low-intensity cereal farming system in central Spain. Weed species richness was negatively influenced by sowing density, herbicides and surrounding mean field size. Carabid species richness was negatively related to applied nitrogen, but positively to surrounding land cover diversity and applied phosphorous. Bird species richness was positively influenced by focal field size, but negatively by surrounding land cover diversity, sowing density and amount of potassium applied. Although all three biological groups reflected the influence of intensification factors operating at different spatial scales, the most relevant factors were specific to each particular group. These results have implications in terms of the selection of targets for agri-environmental measures aiming at reversing the impacts of agricultural intensification on biodiversity.

Keywords: Agricultural intensification; High Nature Value cereal systems; Biodiversity; Mediterranean; Spain.

Introduction

Reduction of habitat heterogeneity due to farming intensification has been proposed as a critical process to understand biodiversity responses to agricultural change (Benton et al., 2003). The spatial scales of the induced changes and the specificities of their consequences vary according to different biological groups, factors and farming systems (Tscharntke et al., 2005). As a consequence detailed information on the relative effects on biodiversity of specific management factors is not always available. The lack of sound and unequivocal information in this regard is hampering the design of adequate management prescriptions for agri-environmental programs, whose effectiveness on biodiversity protection remains unclear (Kleijn and Sutherland, 2003).

In Spain, low-intensity cereal farming systems cover 20 % (10 million ha) of the country, harboring one of the most singular and valued bird communities in the European context: the birds of the cereal steppes (Suárez et al., 1997). Due to climate and soil constraints, and the likely adoption by farmers of cost-minimization strategies in relation to CAP payments (Oñate et al., 2007), the level of intensification of pseudo-steppes has remained generally low in comparison to NW Europe (Bignal and McCracken, 1996). In spite of this, most cereal-steppe bird species have experienced marked population declines coinciding with agricultural changes in recent decades (Santos and Suárez, 2005).

Efforts towards understanding the impacts of agricultural intensification in Mediterranean cereal systems have traditionally focused on studying the habitat selection of their main bird species

(see review in Santos and Suárez, 2005). Only recently, has research begun to focus on the relative importance of specific farm level management factors, usually considering just single components of intensification and particular biological groups. Some examples are the responses of birds to irrigation (Brotons et al., 2004) and stubble management (Suárez et al., 2004), and the responses of weeds to different tillage regimes (Mas and Verdú 2003) and organic farming (Romero et al., 2008). Only in the context of a European-wide evaluation of agri-environmental schemes was variation of different groups simultaneously considered (Kleijn et al., 2006), but the relative effect of the different schemes' prescriptions was not differentiated. In all, although there is a consensus on the general threats imposed by agricultural intensification, the relative role of the different intensification factors on each biodiversity component remains unclear.

In this study an explanatory approach was adopted aimed at understanding the variability of weed, carabid and bird species richness in relation to agricultural intensification in a high conservation value cereal dryland in central Spain. Commonly used field-level management factors and surrounding landscape context variables were considered. An information theory-based multimodel inference method was used identify those factors more clearly influencing the observed species richness of these three biological groups. Hypotheses were that the most relevant intensification factors should be specific to each particular group, although all three should reflect the influence of factors operating at different spatial scales.

Methods

The study was conducted in a 900 km^2 flat to gently undulated area in central Spain (40º 40' N, 3º 25' W). Average annual temperature is 14.1 ºC with hot summers (average max. 33 °C) and mild winters (average min. 0.3 °C) and average annual rainfall is 386 mm, concentrated in spring and autumn (1971–2000; AEMET, 2008). As in other cereal drylands, traditional land use has produced a dynamic agricultural mosaic in the area, with fields of different size (in the range 0.5-30 ha) and varying development of field boundaries. Non-irrigated winter wheat and barley (hereafter, arable crops) and annual fallow (fields not sown in a given year; hereafter, fallow) are dominant, covering *ca.* 86% of total area. The rest is long-term fallow (more than two year old), shrubs and, marginally (0.60% of total area), olive groves and vineyards. Typical rotation on a given field has a two-year cycle, with alternating cereals and fallow. Cereal yield in the study area is around 3000 kg ha^{-1}, lying within the range of central Spanish drylands (average ± SD is 3256 ± 710 kg ha^{-1}; MARM, 2008), but still low enough to consider this system as low-intensity in the European context (Bignal and McCracken, 1996). On the basis of its important cereal-steppe bird populations, the study area is almost entirely included in the proposed Site of Community Interest "Jarama and Henares Steppes", designated under the EU's Birds Directive. No management plan for this Natura 2000 site is in force to date.

Sampling

Weeds, carabids and birds were used to estimate biodiversity on the basis of their wide range of species, sufficiently distinct as to

their size, mobility and ecological requirements. As a measurement of biodiversity, species richness was selected because of its simplicity and sensitivity to processes acting at local and larger spatial scales on species differing in size and mobility.

Field work was conducted in spring 2007, an average year regarding temperatures and rainfall in the area (MMA, 2008). Thirty 1 x 1 km squares were randomly located in the study area, and five points for sampling weeds and carabids were distributed over one to four arable fields inside each square. In total 150 sampling points were distributed over 78 fields. Selected fields were all sown with winter wheat to minimize the influence of crop type or canopy structure on measured biodiversity. Selected fields within each square belonged to the same farmer, involving a total of 15 different farmers. To avoid field margin effects on observations, sampling points were positioned 10 m from the centre of one side of the field. Whenever two sampling points coincided in the same field, they were placed at opposite sides of that field.

Weed species were surveyed between May 27th and June 25th. Three 2 x 2 m vegetation quadrats per sampling point were located. Quadrats were placed parallel to the field side and five meters apart from each other. To minimize the effect of varying abundance of individuals, the species richness recorded in each field were successively averaged to arrive at a weed species richness value per 1 x 1 km square.

Table 1. Description and summary statistics of field management and landscape context factors (N = 30).

Variable	Description	Mean ± SD
Field size (Fsize)	Focal field size (ha)	5.48 ± 5.34
Mechanical weed control (Mcwc)	Number of yearly soil disrupting operations performed with machinery to control weeds	3.51 ± 1.42
Herbicide (Herb)	Rank composite index integrating toxicity of active components (A, B, C), dose (kg ha^{-1}) and number of applications (max.: 9; min.: 0)	-
N fertilizers (N)	Total nitrogen applied on focal fields (kg ha^{-1})	60.37 ± 35.03
P fertilizers (P)	Total phosphorous applied on focal fields (kg ha^{-1})	67.84 ± 57.59
K fertilizers (K)	Total potassium applied on focal fields (kg ha^{-1})	30.88 ± 14.79
Sowing density (Sowd)	Density of seed sown in focal fields (kg ha^{-1})	208.87 ± 73.69
Yield (Yield)	Cereal grain obtained in focal field (ton ha^{-1})	3.14 ± 1.24
Mean field size (Mfs)	Mean size (ha) of every field with cereal crops inside a circle radius 500 m centered in the sampling point	3.97 ± 4.68
Land cover diversity (Lcd)	Shannon index (H') of land cover classes inside a circle radius 500 m centered in the sampling point	0.87 ± 0.29

All factors adjust to a normal distribution (Kolmogorof-Smirnov test, $P < 0.05$) except Sowd and Mfs, which were ln (x+1) transformed. Organic fertilizers were only applied on three sampled fields, in the form of sewage sludge with 153 kg N ha^{-1}, 300 kg P ha^{-1} and 25 kg K ha^{-1}.

Surface-dwelling carabid species were surveyed using pitfall traps 90 mm in diameter and filled with 50% ethylene glycol. Two traps per sampling point were located, parallel to the field side and 10 m apart from each other. Traps remained opened during two one-week periods, 1-8 May and 1-8 June. Captured specimens were fixed with 70% ethanol. All species caught in one trap randomly selected from each pair of traps were identified. As for weeds, richness values were

successively averaged to arrive at a carabid species richness value per 1 x 1 km square.

Birds were surveyed three times during the local breeding period (April 15th – June 15th), approximately every three weeks, in areas of 500 x 500 m centered in one of the focal fields within each 1 x 1 km square. To avoid spatial autocorrelation, focal fields from different squares were at least one kilometer apart. Surveys took place between one hour after dawn and until noon, but only if it was not windy, cloudy, or raining, and were conducted by slowly walking the entire census area, so that each spot was no further than 100 m from the surveyor's route. In order to minimize bias in species richness counts, only cereal steppe specialists and species known to breed in the area were taken into account, migrant and/or occasional species being discarded. Given the generally lower number of individuals and detectability of bird species compared to carabids or weeds, total species richness over the three census rounds in each area was considered.

Information on eight common agricultural management factors was gathered at the field level at the end of the season through questionnaires to farmers owning each of the sampled focal fields: field size, frequency of mechanical arable weed control, herbicide use, applied amount of nitrogen (N), phosphorus (P) and potassium (K) as fertilizers, sowing density, and yield. Herbicide use was estimated by means of a rank index. Its calculation included not only applied amounts (kg ha^{-1}) and frequency of herbicide applications, but also an indication of the standard toxicity attributed to the active components in the particular product used by each farmer. Data for each factor at

the field-level were averaged considering those focal fields within each 1 x 1 km square. Averaged values over the 30 squares reflect the low-intensity character of the studied farming system (Table 1).

Landscape context was characterized through 13 variables referred to the main features of its composition and structure. Landscape variables were measured within a 500 m-radius circle centered on each sampling point, using digitized maps from ortho-images of the study area and Patch Analyst 3.12 extension to ArcView (see Rempel et al., 1999). Data on each variable were averaged considering sampling points within each 1 x 1 km square. Principal component analysis on the resulting matrix showed that a large part of landscape complexity was captured by variation in mean field size and land cover diversity (Supplementary Material, Table A1). In consequence, these two variables were used as landscape factors (Table 1).

Analysis

Bird, carabid, and weed richness were used as response variables (30 observations each), while the 10 factors were used as explanatory variables (30 observations each). To avoid the geographical component showed by response variables, residuals of the regressions of UTM coordinates to each of them were used instead of the original data. In all three cases the residuals adjusted to a normal distribution (Kolmogorov-Smirnov test; $p > 0.05$; Supplementary Material, Table A3).

General Linear Models were applied to analyze, separately for each response variable, the factors explaining most variance. In each case, all possible permutations of the factors were tested and all significant

models were ranked by the Akaike Information Criterion corrected for small sample size (AIC_c, see Burnham and Anderson, 2002). Akaike weights (W_i), representing the relative probability for a model i to be the best among considered models, were calculated for the subset of models having Δ_i (AIC_{best}-AIC_i) ≤ 3. In a model averaging procedure averaged parameters and their corresponding unconditional standard errors were calculated from the smallest subset of AIC_c-ranked models for which ΣW_i was ≥ 0.95. Then, the relative importance of each factor within the averaged model was estimated by summing Akaike weights of those models within the 95% confidence set containing that factor. Factors yielding $\Sigma W_i \leq 0.3$ were neglected in terms of the significance of their effect on response variables. Several factors showed significant ($p < 0.05$) inter-correlations, although Pearson correlation coefficients were never > 0.7 in these cases (Supplementary Material, Table A4). However, the averaging procedure is robust to the potential problem of variable collinearity, and at the same time avoids the loss of explanatory power caused by dropping these variables from the analysis (Graham, 2003). All analyses were performed with Statistica 8.0 (StatSoft, 2007).

Results

Species richness and model averaging

A diverse bird assemblage was recorded, including 14 cereal steppe specialists and six generalist species known to breed in the area (Supplementary Material, Table A5). Average species richness (± SE) per 500 x 500 m census area was 7.34 ± 2.54. The conservation interest of this cereal system was reflected by the European threat status of

recorded species (BirdLife International, 2004), with only five of them classified as "Secure" and four classified as "Vulnerable": great bustard *Otis tarda*, little bustard *Tetrax tetrax*, northern lapwing *Vanellus vanellus*, and stone-curlew *Burhinus oedicnemus*.

Table 2. Results of information theory-based model selection and multimodel inference for bird species richness in the study area.

Model	Fsize	Mcwc	Herb	N	P	K	Sowd	Yield	Mfs	Lcd	AIC_c	ΔAIC_c	W_i
1	X					X					84.23	0.00	0.117
2	X						X			X	84.43	0.19	0.097
3	X					X				X	84.54	0.30	0.092
4						X				X	85.10	0.87	0.069
5	X										85.18	0.95	0.067
6	X									X	85.38	1.14	0.060
7	X			X		X					85.98	1.75	0.045
8	X					X	X			X	86.06	1.83	0.043
9						X			X	X	86.16	1.93	0.041
10		X					X			X	86.22	1.98	0.040
11	X	X					X			X	86.25	2.01	0.039
12	X			X	X		X			X	86.34	2.10	0.037
13	X				X		X			X	86.44	2.20	0.035
14	X			X		X				X	86.61	2.38	0.033
15		X					X		X	X	86.78	2.54	0.030
16		X		X			X			X	86.79	2.55	0.030
17	X		X				X			X	86.87	2.64	0.029
18	X			X			X			X	86.88	2.64	0.028
19	X						X	X		X	86.89	2.65	0.028

The 95% confidence set of models (for which sum of Akaike weights is ≥ 0.95) are detailed. Inclusion of factor in each individual model is indicated with X. Akaike's information criterion corrected for small sample size (AIC_c), the AICc differences compared with the most parsimonious model (ΔAIC_c) and Akaike weights (W_i) are given for each model. See Table 1 for definition of factors.

The recorded carabid assemblage included 36 species, with an average species richness per 1 x 1 km square of 2.43 ± 1.05

(Supplementary Material, Table A6). None of them was listed under the Habitat Directive or the Spanish legislation on threatened species.

Table 3. Results of information theory-based model selection and multimodel inference for carabid species richness in the study area.

Model	Fsize	Mcwc	Herb	N	P	K	Sowd	Yield	Mfs	Lcd	AIC_c	ΔAIC_c	W_i
1				X	X					X	79.023	0.000	0.278
2				X	X		X			X	80.462	1.440	0.136
3		X		X	X					X	80.954	1.932	0.106
4				X	X				X	X	81.269	2.246	0.091
5			X	X	X					X	81.318	2.295	0.088
6				X	X	X				X	81.363	2.340	0.086
7				X	X			X		X	81.413	2.390	0.084
8	X			X	X					X	81.523	2.500	0.080

The 95% confidence set of models (for which sum of Akaike weights is ≥ 0.95) are detailed. Inclusion of factor in each individual model is indicated with X. Akaike's information criterion corrected for small sample size (AIC_c), the AICc differences compared with the most parsimonious model (ΔAIC_c) and Akaike weights (W_i) are given for each model. See Table 1 for definition of factors.

A total of 107 weed species were identified (Supplementary Material, Table A7), with an average species richness per 1 x 1 km square of 10.97 ± 4.39. None of them was listed under the Habitat Directive or the Spanish legislation.

The AIC-based selection process included 19 models in the 95% confidence set for bird species (Table 2), while eight and 16 models were included respectively in the cases of carabids (Table 3) and weeds (Table 4). None of the "best" simple model for each response variable showed relevant differences in their AIC_c values compared to the rest of models, which confirmed the adequacy of the model averaging procedure in all cases.

Table 4. Results of information theory-based model selection and multimodel inference for arable plant species richness in the study area.

Model	Fsize	Mcwc	Herb	N	P	K	Sowd	Yield	Mfs	Lcd	AIC_c	ΔAIC_c	W_i
1			X				X				78.526	0.000	0.139
2			X			X	X		X		79.320	0.794	0.093
3			X				X	X	X		79.325	0.800	0.093
4			X				X	X			79.379	0.853	0.091
5			X				X		X		79.414	0.888	0.089
6			X			X	X				79.633	1.108	0.080
7	X		X				X				80.551	2.025	0.050
8			X	X			X				80.920	2.394	0.042
9			X		X		X				80.937	2.411	0.042
10			X				X			X	80.940	2.415	0.042
11		X	X				X				80.962	2.436	0.041
12			X		X		X	X	X		81.269	2.743	0.035
13	X		X		X		X		X		81.342	2.816	0.034
14			X			X	X	X			81.342	2.816	0.034
15			X			X	X	X	X		81.388	2.862	0.033
16	X		X				X	X			81.414	2.889	0.033

The 95% confidence set of models (for which sum of Akaike weights is ≥ 0.95) are detailed. Inclusion of factor in each individual model is indicated with X. Akaike's information criterion corrected for small sample size (AIC_c), the AICc differences compared with the most parsimonious model (ΔAIC_c) and Akaike weights (W_i) are given for each model. See Table 1 for definition of factors.

Factors influencing species richness

The three biological groups reflected the influence of factors at both spatial scales (field and landscape), but those with a higher effect were different in each case (Table 5). Sowing density, herbicide application and surrounding mean field size had a negative influence on weed species richness. Other factors were negligible, except perhaps the case of yield, for which $\Sigma W_i = 0.29$.

Variation in carabid species richness was best explained by the amount of applied N, showing a negative influence, and the amount of

P and land cover diversity in the surroundings, with a positive influence. Other factors in the averaged model were $\Sigma W_i < 0.3$.

Bird species richness was positively influenced by focal field size, and negatively by sowing density, applied amount of K and surrounding land cover diversity. Other factors in the averaged model were $\Sigma W_i < 0.3$.

Table 5. Parameter (*βprom*) values and their unconditional standard errors (USE) for the different factors in the three averaged models.

	Birds		Carabids		Arable weed	
	βprom	USE	*βprom*	USE	*βprom*	USE
Fsize	0.046	0.026				
Mcwc						
Herb					-0.189	0.054
N			-0.016	0.006		
P			0.012	0.003		
K	-0.009	0.007				
Sowd	-0.376	0.351			-1.574	0.546
Yield					-0.00005	0.00009
Mfs					-0.255	0.373
Lcd	-0.854	0.508	1.369	0.492		

Only factors for which sum of Akaike weights over models within the 95% confidence set containing that factor was ≤ 0.3 are sown, except Yield (0.29). See Table 1 for definition of factors.

Discussion

None of the 11 considered factors contributed to explain variability in species richness of all three groups simultaneously. This specificity would question the use of single indices as meaningful and general proxies for assessing the effects of intensification on biodiversity. The role of yield was particularly deceptive in this sense. Although yield is

usually taken as a reliable correlate of agricultural intensification (e.g. Green et al., 2005), in this study it only showed a limited explanatory power for weed richness variation. Yield variability was small and probably reflected the constraints imposed by climate and soil limitations, irrespective of the intensification efforts of individual farmers (see Table1). This is a frequent circumstance in Spanish drylands (Oñate et al., 2007), where yield could be a misleading proxy for intensification, especially if considered at local scale.

Field level

Sowing density negatively influenced bird and weed richness. Its relation to birds has also been found in NW European cereal farmland, where accessibility to food by seed-eaters (Butler et al., 2005) and insectivorous birds (Odderskaer et al., 1997) was found to diminish in uniform and dense swards. The detected relationship is also consistent with habitat selection studies from Spain, where sparsely vegetated ground is generally favored for nesting and foraging by species dependent on early detection of approaching predators (see review in Santos and Suárez, 2005). In the case of weeds, this relationship probably reflects the disproportionate advantage of larger plants (crop plants) in competition with smaller plants (weeds). This is consistent with research evidencing that the advantage of size in competition increases with density (Schwinning and Weiner, 1998). Interestingly, the case of sowing density illustrates a plausible paradox mediated by likely management decisions to combat weeds. Sowing at high seed density would seem reasonable from the agronomic and environmental points of view (Weiner et al., 2001) given the financial saving and pollution

avoidance derived from a reduced use of energy-intensive forms of weed control (mechanical or chemical). But according to results presented here, sowing at higher seed density would imply a negative counterpart in terms of diminished structural suitability of the cropland habitat for pseudo-steppe birds.

Surprisingly, nutrients were unimportant in explaining weed richness. It is likely that farmers apply fertilizers more intensively when sowing at higher densities, but the negative influence of the latter on weed richness seems to prevail over the expected positive effect of fertilizers. As to carabids, a negative influence of chemical fertilization, mediated by lowered prey abundance, has been demonstrated elsewhere (e.g. Bengtsson et al., 2005), although the effects of different inorganic nutrients were not distinguished. Our results corroborated this negative influence for the case of N fertilization, but the contrary was detected for the amounts of P. This is a striking result, but since food availability is just one the factors influencing richness of carabid species (e.g. Holland, 2002), it can be reasonably argued that P affects other factors, such as sward structure and micro-climate, which in turn are detrimental for carabids. As to birds, it seems that the effects of fertilizers would mainly be mediated by the more uniform and dense swards that fertilisation promotes, thus indirectly impacting on them as it has been discussed above. Only for the case of K a direct negative influence was found.

Also relevant at the field level, the expected negative influence of higher values of the utilized rank herbicide index on weeds was confirmed. In contrast, weeds were not affected by the frequency of mechanical weed control.

Finally, the influence of focal field size was only detected in the case of birds, whose species richness was higher in larger fields. The well-known species-area relationship would be the simplest explanation, but the micro-habitat selection of cereal-steppe bird species, known to favor sites of high visibility (Santos and Suárez, 2005) should also be taken into account. The more extensive area distant from field borders (and human tracks) in larger fields would allow earlier detection of approaching predators (or human disturbances) and therefore increased chances to escape.

Landscape level

Often promoted through land consolidation projects, enlargement of field size aims to maximize the operation efficiency of agricultural machinery and reduce management costs in arable systems (but see Rodríguez and Wiegand, 2009). Field enlargement implies the concomitant elimination of field boundaries, marginal areas and habitat patches and a reduction of crop types (e.g. Baessler and Klotz, 2006), lowering land cover diversity. However, both factors were not statistically correlated in the data set, and they proved distinctively important for different groups.

As in NW European cereal systems, surrounding land cover diversity proved beneficial to carabid richness in this study. A more diversified land cover has been linked to increased dispersal opportunities and variety of potential immigration sources, both in terms of crop diversity and field boundaries (Östman et al., 2001) and the proportion and connectivity of semi-natural elements in the landscape (Schweiger et al., 2005). Contradictorily, the same factor showed a negative influence on bird richness. To understand this

result, it is important to consider the high spatial continuity of the habitat typically selected by most Mediterranean cereal-steppe birds (Santos and Suárez, 2005). In the studied area, cereal crops and fallow land extend over 86 % of the territory, and the values of land cover diversity are generally low. Only in those cases with occasional presence of permanent crops, natural vegetation or built-up areas were higher values found. But these are precisely the land cover types known to be detrimental for cereal-steppe specialist bird species (Díaz and Tellería, 1994). The contrasting responses of birds and carabids to land cover diversity are most probably related to the different scales at which these groups experience the relatively simple farmed landscape, given their different habitat requirements and dispersal abilities (Tscharntke et al., 2005).

Mean field size in the surroundings negatively influenced weed richness sampled on focal fields. Weeds are known to rely not only on their seed bank, but also on immigrating seeds from field boundaries (Romero et al., 2008). As mentioned above, the density of field boundaries is usually diminished as mean field size increases in any given landscape. Therefore, diminished neighborhood effects could lie behind the detected negative association, due to lowered immigration of species from surrounding habitats appropriate for annual and ruderal plants (Gabriel et al., 2005). However, richness of bird species on focal fields did not respond to variation of surrounding mean field size, in spite of previous research reporting a negative relation between both elsewhere in NW Europe (e.g. Belfrage et al., 2005). It is most probable that the low values and modest variability of field size in the studied system lie behind this lack of significance (surrounding fields in the sampled buffers

ranged from 0.96 ha to 24.02 ha, and the median was just 2.45 ha, with only two cases above 13 ha).

Management implications

Previous research has evidenced the low effectiveness of Spanish agri-environmental schemes in terms of biodiversity enhancement in this type of low-intensity cereal systems (Kleijn et al., 2006). This is partly due to the poor design of prescribed management measures, whose coverage of agricultural habitat conservation requirements in these systems is inadequate (Llusia and Oñate, 2005). In particular, these measures rarely take into account the distinctive scale-dependent response of target species to a given prescribed management (Concepción et al., 2008).

The design of agri-environmental measures aiming at enhancing the biodiversity value of these singular systems should take into account the varied factors-group links and the spatial scales at which they operate. The possibility that certain management measures have contrasting effects on different biodiversity components in the system is a complication that should be taken into account. The direct extrapolation to Mediterranean cereal agro-ecosystems of factors-group relationships reported in temperate Europe could be misleading if taken as the basis for management recommendations.

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Supplementary information

Table A1. Factor loadings, eigenvalues and absorbed variance after unrotated PCA on considered agricultural landscape variables. *N* = 30 in all cases.

Variable	Factor 1	Factor 2
Cereal crops (%)	-0.935	-0.069
Permanent crops (%)	0.123	-0.202
Fallow land (%)	0.647	-0.283
Pastures (%)	0.688	0.390
Natural vegetation (%)	0.236	-0.299
Water (%)	0.421	0.432
Built areas (%)	0.346	0.672
Shannon land cover diversity index (H')	0.921	0.270
Mean cereal field size (ha)	0.240	-0.786
Mean cereal field size SD (ha)	0.086	-0.878
Mean field boundary density (m/ha)	-0.631	0.423
Mean field shape index	-0.433	0.266
Mean field fractal dimension	0.340	-0.155
Eigenvalue	3.753	2.799
Total variance (%)	28.872	21.531

Table A2. Results from the analysis of geographical component (UTM coordinates x, y) in explanatory factors. Direction of association (- or +), Wald statistic (*W*) and *p*-value are given only for statistically significant results from GLM analysis. *N* = 30 in all cases.

Variable	Coord. x	*W*	*P*-value	Coord. y	*W*	*P*-value
Focal field size	+	6.243	0.012			
Mechanical weed control						
Herbicide	-	3.941	0.047	+	10.371	0.001
N fertilizers						
P fertilizers						
K fertilizers						
Sowing density						
Yield	-	9.275	0.002	-	4.411	0.035
Mean field size	+	14.362	0.0001			
Land cover diversity						

Table A3. Results from multiple regressions of bird, carabid and weed richness on UTM coordinates (x, y). Explained variation (R^2), *F*-test (df) and *P*-value are given for each model. Regression coefficient (*Beta*), *t*-value and resulting *p*-value for statistically significant cases are in bold. (*N* = 30 in all cases).

Variable	R^2	*F*(2,27)	*p*-value	*Beta*	*t*(27)	*p*-value
Bird richness	0.234	4.127	0.027			
Coord. x				0.284	1.621	0.116
Coord. y				**0.479**	**2.732**	**0.011**
Carabid richness	0.254	4.608	0.019			
Coord. x				**0.515**	**2.975**	**0.006**
Coord. y				0.045	0.261	0.795
Weed richness	0.051	0.726	0.492			
Coord. x				-0.155	-0.793	0.434
Coord. y				0.126	0.647	0.523

Table A4. Correlation matrix (Pearson correlation coefficients) including all field management and landscape variables: Focal field size (Fsize), Yield, Herbicide application (Herb), Sowing density (Swod), Amount of N, K and P fertilizer (N, K and P), frequency of mechanical weed control (Mcwc), Surrounding mean field size (Mfs) and land cover diversity (Lcd). Only statistically significant correlations ($p < 0.05$) are shown. N = 30 in all cases.

	Fsize	Yield	Herb	Swod	N	P	K	Mcwc	Mfs	Lcd
Fsize	1.000									
Yield		1.000								
Herb			1.000							
Swod		0.456	-0.412	1.000						
N		0.564		0.407	1.000					
P					0.634	1.000				
K		0.662		0.473	0.503		1.000			
Mcwc	-0.392		0.434					1.000		
Mfs	0.648								1.000	
Lcd										1.000

Table A5. Latin and common names of recorded bird species and number of 500 x 500 m census areas (N = 30) where each species was recorded. European threat status according to BirdLife International (2004).

Latin name	Common name	Threat status	Number
Alauda arvensis	Skylark	Declining	4
Alectoris rufa	Red-legged partridge	Declining	27
Anas platyrhynchos	Mallard	Secure	12
Anthus campestris	Tawny pipit	Depleted	4
Anthus pratensis	Meadow pipit	Declining	6
Burhinus oedicnemus	Stone-curlew	Vulnerable	6
Calandrella brachydactyla	Short-toed lark	Vulnerable	1
Circus aeruginosus	Marsh harrier	Secure	13
Circus pygargus	Montagu's harrier	Secure	9
Cisticola juncidis	Fan-tailed warbler	Secure	28
Coturnix coturnix	Common quail	Secure	12
Galerida cristata	Crested lark	Depleted	30
Melanocorypha calandra	Calandra lark	Depleted	4
Miliaria calandra	Corn bunting	Declining	29
Motacilla flava	Yellow wagtail	Declining	2
Oenanthe oenanthe	Wheatear	Declining	1
Otis tarda	Great bustard	Vulnerable	7
Pterocles orientalis	Black-bellied sandgrouse	Vulnerable	2
Tetrax tetrax	Little bustard	Vulnerable	13
Vanellus vanellus	Lapwing	Vulnerable	5

Table A6. Latin name of recorded carabid species and number (N^{er}) of 1 x 1 km squares ($N = 30$) where each species was recorded.

Latin name	N^{er}	Latin name	N^{er}
Acinopus picipes	2	*Harpalus distinguendus distinguendus*	5
Acupalcus brunnipes	3	*Harpalus oblitus patruelis*	4
Amblystomus niger	1	*Laemostenus baeticus*	1
Anchomenus dorsalis	1	*Microlestes corticallis*	2
Asaphidion curtum	1	*Microlestes minutulus*	18
Bembidion ambiguum	12	*Nebria salina*	2
Bembidion tethys	1	*Orthomus sp.*	7
Brachinus explodens	5	*Parophonus hispanus*	12
Brachinus immaculicornis	4	*Platytarus bufo*	1
Calathus cinctus	1	*Poecilus crenulatus crenulatus*	10
Calomera littoralis nemoralis	1	*Poecilus cupreus cupreus*	2
Calosoma maderae maderae	4	*Poecilus gisellae gisellae*	4
Carterus rotundicollis	7	*Poecilus kugelanni*	1
Chlaenius chrysocephalus	10	*Poecilus purpurascens purpurascens*	29
Chlaenius decipiens	1	*Pterostichus globosus ebenus*	22
Demetrias atricapillus	1	*Siagona europaea europaea*	1
Dyschirius semistriatus	1	*Trechus quadristriatus*	14
Gynandromorphus etruscus etruscus	2	*Zabrus gravis*	6

Table A7. Latin name of recorded weed species and number (N^{er}) of 1 x 1 km squares ($N = 30$) where each species was recorded.

Latin name	N^{er}	Latin name	N^{er}
Aegilops triuncialis	2	*Lathyrus angulatus*	5
Agrostis pourretii	3	*Leontodon taraxacoides*	12
Alopecurus myosuroides	2	*Linaria spartea*	12
Anacyclus clavatus	18	*Linum strictum*	5
Anagallis arvensis	6	*Lolium rigidum*	30
Anchusa azurea	1	*Lotus conimbricensis*	2
Andryala integrifolia	11	*Lupinus angustifolius*	2
Anthemis arvensis	4	*Mantisalca salmantina*	1
Aphanes arvensis	2	*Medicago orbicularis*	2
Avena sterilis	27	*Melilotus indicus*	1
Bartsia trixago	5	*Ornithopus compressus*	6
Bromus diandrus	28	*Papaver rhoeas*	18
Bromus hordeaceus	10	*Parentucellia latifolia Carue*	1
Bromus madritensis	6	*Picnomon acarna*	11
Bromus rubens	1	*Plantago coronopus*	4
Bromus sterilis	1	*Plantago lagopus*	2
Bromus tectorum	16	*Polycarpon tetraphyllum*	1
Buglossoides arvensis	4	*Polygonum aviculare*	18
Bupleurum rotundifolium	1	*Polypogon monspeliensis*	2
Campanula erinus	1	*Ranunculus arvensis*	2
Campanula lusitanica	5	*Ranunculus trilobus*	1
Capsella bursa-pastoris	5	*Raphanus raphanistrum subsp. raphanistrum*	16
Carduus tenuiflorus	14	*Rapistrum rugosum subsp. rugosum*	10
Carthamus lanatus	13	*Reseda luteola*	1
Caucalis platycarpos	3	*Rumex pulcher*	1
Centaurea cianus	1	*Senecio vulgaris*	4
Centaurea melitensis	1	*Silene gallica*	1
Cerastium glomeratum	2	*Silene muscipula*	1
Chamaemelum mixtum	18	*Silybum marianum*	17
Chenopodium album	11	*Sonchus asper*	8
Chondrilla juncea	16	*Sonchus oleraceus*	6
Cirsium vulgare	2	*Spergularia purpurea*	10
Cnicus benedictus	5	*Spergularia rubra*	2
Convolvulus arvensis	19	*Stellaria media*	2
Conyza canadensis	11	*Taeniatherum caput-medusae*	8
Coronilla scorpioides	3	*Tolpis barbata*	2
Corynephorus fasciculatus	3	*Tragopogon dubius*	2
Crepis biennis	3	*Trifolium angustifolium*	2
Crepis capillaris	10	*Trifolium arvense*	12
Echium plantagineum	7	*Trifolium campestre*	10

Table A7. Cont.

Latin name	N^{er}	Latin name	N^{er}
Erysimum repandum	1	*Trifolium gemellum*	1
Euphorbia serrata	10	*Trifolium glomeratum*	8
Filago gallica	5	*Trifolium lappaceum*	2
Filago pyramidata	27	*Trifolium resupinatum*	1
Filago vulgaris	6	*Trifolium tomentosum*	4
Galium murale	11	*Trisetum paniceum*	3
Galium tricornutum	14	*Veronica hederifolia subsp. hederifolia*	4
Geranium molle	1	*Vicia lathyroides*	1
Hordeum murinum subsp. leporinum	15	*Vicia lutea subsp. lutea*	6
Hordeum vulgare	28	*Vicia sativa*	9
Hypochoeris glabra	11	*Vulpia ciliata*	5
Juncus bufonius	11	*Vulpia muralis*	4
Lactuca serriola	24	*Vulpia myuros*	7
Lamium amplexicaule	4		

CAPÍTULO II

Diversidad taxonómica y funcional de las comunidades de aves ligadas a los medios agrarios de Europa: efectos de la biogeografía y la intensificación agraria.

Este capítulo reproduce íntegro el siguiente manuscrito:
Guerrero,I.; Morales,M.B.; Oñate,J.J.; Aavik,T.; Bengtsson,J.; Berendse,F.; Clement,L.W.; Dennis,C.; Eggers,S.; Emmerson,M.; Fischer,C.; Florín,M.; Geiger,F.; Hawro,V.; Inchausti,P.; Kalamees,A.; Kinks,R.; Liira,J.; Meléndez,L.; Pärt,T.; Thies,C.; Tscharntke,T.; Olszewski,A. & Weisser,W.W. (2011) Taxonomic and functional diversity of farmland bird communities across Europe: effects of biogeography adn agricultural intensification. Biodiversity and Conservation, 20:3663–3681

Resumen

Utilizando el método de mapeo en cuadrados de muestreo de 500x500 m^2, se obtuvo la abundancia de territorios de aves ligadas a los medios agrarios en ocho áreas de estudio europeas (en España, Irlanda, Holanda, Alemania, Polonia, Estonia y Suecia). Con estos datos, se realizaron dos análisis: (I) un Análisis de Correspondencias Canónicas de abundancia de especies en relación con la localización geográfica y con medidas de intensificación agraria a escala de campo de cultivo y de explotación, para estimar las fracciones de la variación total de abundancia de territorios explicada por la localización geográfica y la intensificación agraria e identificar prácticas agrarias relevantes; (II) se construyeron varios índices taxonómicos y funcionales de las comunidades muestreadas y se analizó, mediante Modelos Lineales, su relación con las variables de intensificación que resultaron significativas en el ACC. La localización geográfica de las zonas de estudio explica por sí sola un quinto (19,5%) de la variación total de la abundancia de especies. La fracción de variación explicada exclusivamente por la intensificación agraria es más pequeña (4,3%) pero significativa. La intersección explica cerca de dos quintos (37,8%) de la variación en la abundancia de especies. Los índices taxonómicos y funcionales están negativamente relacionados con indicadores de intensificación como el tamaño de las explotaciones y el rendimiento agrícola, mientras que indicadores de disponibilidad y calidad de hábitat tienen efectos positivos sobre estos índices. Gran parte de la variación geográfica de la composición de las comunidades estudiadas está asociada a especies esteparias mediterráneas, reflejando la singularidad biogeográfica de estas comunidades, reforzando la necesidad de su conservación. La intensificación agraria afecta negativamente a las diversidades taxonómica y funcional de las comunidades de aves ligadas a estos medios, que se ven favorecidas por la disponibilidad y calidad del hábitat agrícola.

Abstract

In eight European study sites (in Spain, Ireland, Netherlands, Germany, Poland, Estonia and Sweden), abundance of breeding farmland bird territories was obtained from 500 x 500 m survey plots (30 per area, N = 240) using the mapping method. Two analyses were performed: (I) a Canonical Correspondence Analysis of species abundance in relation to geographical location and variables measuring agricultural intensification at field and farm level to identify significant intensification variables and to estimate the fractions of total variance in bird abundance explained by geography and agricultural intensification; (II) several taxonomic and functional community indices were built and analysed using GLM in relation to the intensification variables found significant in the CCA. The geographical location of study sites alone explains nearly one fifth (19.5%) of total variation in species abundance. The fraction of variance explained by agricultural intensification alone is much smaller (4.3%), although significant. The intersection explains nearly two fifths (37.8%) of variance in species abundance. Community indices are negatively affected by correlates of intensification like farm size and yield, whereas correlates of habitat availability and quality have positive effects on taxonomic and functional diversity of assemblages. Most of the purely geographical variation in farmland bird assemblage composition is associated to Mediterranean steppe species, reflecting the bio-geographical singularity of that assemblage and reinforcing the need to preserve this community. Taxonomic and functional diversity of farmland bird communities are negatively affected by agricultural intensification and positively affected by increasing farmland habitat availability and quality.

Keywords: Agriculture management, breeding farmland birds, community indices, Mediterranean, steppe birds, variance partitioning.

Introduction

Farmland is an important habitat for wildlife in Europe, harbouring more than 50% of all European species, including a number of endemic and threatened ones (European Environment Agency 2005). Farmland biodiversity, however, varies considerably across the continent in response to spatial gradients in e.g. climate, soil types and agricultural management (Rosenzweig 1995; Pianka 1996; Hawkins et al. 2003; Robinson and Sutherland 2002 Benton et al. 2003).

At the landscape scale, farmland biodiversity has been related to environmental heterogeneity (Weibull et al. 2000; Tscharntke et al. 2005; Hendrikx et al. 2007), because reduced habitat heterogeneity is often viewed as a key component of the links between changes in agriculture and farmland biodiversity (Benton et al., 2003). However, the relative contribution of specific management factors to this process is not always clear, because the spatial scales at which induced changes operate vary according to different taxa, factors and farming systems (Tscharntke et al., 2005).

Europe comprises very different farming contexts, ranging from extensive dry farmland in the Mediterranean basin to highly intensified agriculture in north-western Europe (Pain and Pienkowski 1997). According to previous work (Donald et al. 2001; Stoate et al. 2001; Robinson and Sutherland 2002) differences in farmland biodiversity along this range can, to a large extent, be attributed to increased intensification from south to north, and from east to west Europe, although evidence obtained over such geographical range under common protocols (thus allowing direct comparisons between localities) is scarce (but see Kleijn et al. 2009; Geiger et al. 2010).

Moreover, although large-scale environmental gradients linked to climate and soil (among others) are expected to influence continent-level changes in farmland biodiversity, no study has so far evaluated the relative contribution to changes in biodiversity of agricultural intensification, on one hand, and geographical differences between study sites in different European countries, on the other. Separating these two effects is relevant to adequately assess the response of biological communities to agricultural intensification and its many components related to farming practices, so that the real state of farmland biodiversity in the different countries can be established. For example, the absence or small abundance of steppe bird species in central Europe as compared to Mediterranean countries cannot be attributed to agricultural intensification without consideration of environmental differences between regions, and vice versa.

Besides species richness and abundance, agricultural intensification may reasonably affect other structural and functional features of farmland biological communities. Intensification may affect more markedly some taxonomic or functional groups than others within species assemblages. Structural and functional changes in communities resulting from habitat degradation have been described in different types of ecosystems (Bradford et al. 1998; Bryce et al. 2002). More recently, several studies have assessed the response of farmland bird communities to habitat fragmentation and disturbance at the landscape level (Devictor and Jiguet 2007; Devictor et al. 2008; Devictor and Robert 2009), showing how the use of indices based on the taxonomic and/or functional composition of assemblages can be applied to evaluate the ecological condition of communities and their habitats, which is a relevant issue in habitat management, ecological

restoration and biodiversity conservation. Nevertheless, no previous study has evaluated the effect of agricultural intensification factors at the field and farm levels on farmland bird taxonomic and functional diversity at continental (i.e. European) scale.

In the present paper, data on the breeding abundance of farmland-specialist birds collected under a common sampling protocol in eight study sites distributed throughout Europe are analysed with two major aims: (i) to assess the relative effect of agricultural intensification and geographical location in the variation of species composition and abundance of the farmland bird assemblage across the continent, and (ii) to identify the variables related to agricultural intensification that more clearly can modify the structural and functional characteristics of European farmland bird assemblages using different measures of community taxonomic and functional diversity.

Methods

Study Area

Bird surveys were carried out in eight study sites located in seven European countries: Sweden, Estonia, Poland, the Netherlands, Germany (2 areas, Göttingen and Jena, based on their contrasted landscape characteristics derived from different land use histories, see Fischer et al., 2011), Spain and Ireland (Figure 1). The size of these areas was relatively homogeneous, ranging from 30 x 30 km to 50 x 50 km. Between 30 to 32 arable land farms were selected per site along an intensification gradient using cereal yield as a proxy for agricultural intensification (see, for example, Geiger et al 2010). Farm

selection proceeded so that cereal yield and landscape composition were uncorrelated within study sites.

Fig. 1. Location of the study sites (black dots) in Sweden, Estonia, Ireland, Netherlands, Germany (Göttingen), Germany (Jena), Poland and Spain.

Bird surveys

To make bird counts comparable, one survey plot of 500 x 500 m in size was selected per farm. Depending on the farm land use characteristics, each survey plot comprised one or more arable field types and/or permanent grasslands, but always included at least one cereal field. Most cereal fields corresponded to winter wheat (79%), the major crop in Europe, although other cereal cultures like barley (9%), spring wheat (6%), winter rye (5%) and triticale (<1%) were also included. All survey plots were at least 1 km apart.

Surveys were performed during spring and summer 2007; starting according to local information on the phenology of breeding birds and repeated two more times at intervals of three weeks. They were conducted according to a modified version of the British Trust for Ornithology Common Bird Census protocol (Bibby et al., 1992). Plots were surveyed so that the longest distance from the surveyor's route to each spot within the quadrat was 100 m. Surveys took place between one hour after dawn and noon, avoiding too windy, cloudy or rainy weather.

Breeding bird territories were determined for ground-nesting farmland birds, that is, those directly nesting on ground or short vegetation, using the three survey rounds. Three different criteria were used to define breeding bird territories, depending on the species' detectability and breeding behaviour (see Appendix Table 4). To meet the criteria for assigning a breeding territory, species of category A had to be observed at least twice displaying territorial behaviour (foraging, calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds. Category B comprised species unlikely to be present during all the three survey visits because of their migration behaviour (e.g., long-distance migrants arriving relatively late) and species considered difficult to observe. For this category, only one observation of territorial behaviour was required. For category C species, direct evidence of breeding activities was required.

Agricultural intensification data

Information about yield and farming practices (farm type, number of crops per farm, perimeter-area ratio, pesticide and fertilizer use,

ploughing and mechanical weed control regime; see Table 1) was collected by means of a questionnaire sent out to all participating farmers. Average completion of questionnaires by all farmers was 98%, although the participation of individual farmers was 100%. Farm structure differed between study sites. Consequently, "farm" was defined as one or more fields cultivated by the same farmer that were no more than 1 km distant from each other. When bird survey plots included land belonging to more than one farm, the intensification data corresponding to the farm covering most part of the plot were used. Information at the farm scale (number of crops, farm type) was based on the total area belonging to that farm, thus always including land outside the survey plot.

Information about farming practices was referred to those carried out in one to five cereal fields (generally winter wheat), depending on their size and number (and thus their availability) in each farm. This means that data about farming practices were averaged over up to five fields with the same cereal type belonging to the same farm.

Landscape characteristics

Two characterizing landscape variables were estimated within circles with a radius of 500 m around the centre of each survey plot: mean field size and the percentage of land planted with arable crops within the area (see Table 1). Within that radius, the following land use classes were used to estimate the habitat diversity, according to the definitions from the European Topic Centre on Land Use and Spatial Information (Büttner et al. 2000): continuous urban fabrics, discontinuous urban fabrics, cultivated arable lands, fallow lands

under rotation systems, permanent crops, pastures, forests, transitional woodland-scrub and water.

Table 1. Description of the agricultural intensification variables considered in Canonical Correspondence Analyses. Asterisks indicate those variables selected by the forward step-wise regression model ($p < 0.05$).

Explanatory variable	Description	Unit	Sampling level	Source
Carabid richness*	Total number of carabid species			Direct observation
Weed richness*	Total number of weed species			Direct observation
Yield*	Assuming 14% moisture content of the grains	Tons ha^{-1}	Field	Questionnaires
Number of crops*	Number of crops cultivated in 2007	$Farm^{-1}$	Farm	Questionnaires
Agri-environment schemes*	% area of farm with agri-environment scheme	%	Farm	Questionnaires
Farm size*	Amount land held by the same owner	Ha	Field	Questionnaires
Field size	Size of sampled field	Ha	Field	
Insecticide*	Number of applications	y^{-1}	Field	Questionnaires
Herbicide	Number of applications	y^{-1}	Field	Questionnaires
Fungicide	Number of applications	y^{-1}	Field	Questionnaires
N fertiliser*	Total amount of inorganic nitrogen fertiliser	Kg N ha^{-1} $year^{-1}$	Field	Questionnaires
Organic fertiliser	Total amount of organic fertiliser	Kg N ha^{-1} $year^{-1}$	Field	Questionnaires
Soil disrupting*	Frequency mechanical soil disrupting operation (Weed control, ploughing)	$Year^{-1}$	Field	Questionnaires
Mean field size in landscape*	mean field size within 500m radius measured around sampling points	Ha	Landscape	Direct observation
Cereal surface in landscape*	% arable crop within 500m radius measured around sampling points	%	Landscape	Direct observation

Data treatment and analyses

The number of territories of the different farmland bird species identified at each survey plot was used as a measure of ground-nesting breeding bird abundance (hereafter, species abundance). Unimodal Canonical Correspondence Analysis (CCA) was used to examine relationships between the abundance of all breeding birds and the different intensification variables. CCA is a constrained non-linear ordination method, analogous to a multiple regression for all species abundances simultaneously, where explanatory variables are limited to being a combination of the recorded intensification variables. Therefore, this analysis is robust to moderate violation of the assumptions of a normal distribution (Leps and Smilauer 2003), although, nevertheless, prior to the canonical ordination analysis, each intensification variable was checked for normality, and transformed when necessary.

The study site (geographical location) was included in the analysis as a covariable through transformation into dummy variables. Intensification variables (or explanatory variables) were selected by means of a forward step-wise regression based on Montecarlo permutation tests (999 permutations) on canonical ordination axes, in which only significant variables ($\alpha < 0.05$) were used in the final model (Leps and Smilauer 2003).

The significance of the contribution of canonical axes to explain the variation in species abundance was tested by means of regression analyses. The variation explained by the canonical axes associated to agricultural intensification and study site was used, in a variance partitioning procedure, to identify the proportion of total variance

explained purely by agricultural intensification and by geographical location (Leps and Smilauer 2003). This procedure required testing the significance of four different regression models of species abundance with Montecarlo permutations (n= 999) in relation to: (i) intensification variables, (ii) study site, (iii) intensification variables including study site as covariable, and (iv) study site including intensification variables as the covariable matrix. The global results of the ordination were additionally confirmed by examination of graphs of species versus environmental variables (biplot species-environmental variables). Analyses were performed with the CANOCO 4.5 software (Ter Braak and Smilauer 2002).

Several community indices based on species taxonomy, co-occurrence and functional traits were built to describe the ecological state of farmland bird assemblages in terms of taxonomic and functional diversity and habitat suitability. Species richness is used as a simple and direct measure of taxonomic diversity (Krebs 1994). A taxonomic distinctiveness index was built following Warwick and Clarke (1998) and von Euler and Svensson (2001). This index is based on between-species phylogenetic distances obtained from Sibley and Ahlquist (1990) and Sibley and Monroe (1990) and can be interpreted as a measurement of phylogenetic diversity within assemblages: from assemblages including a variety of closely and far-related species to assemblages dominated by closely related species (see Warwick and Clarke 1998 and von Euler and Svensson 2001 for applications in community ecology). Also, a co-occurrence index based on the number of survey squares in which two given species co-occur, divided by the number of squares in which either one or the other occurs (Gotteli et al. 1997; von Euler and Svensson

2001), was used as a measure of the assemblage average pair-wise separation by survey squares, reasonably assuming that if any two species tend to occur together in most squares, then the habitat quality of most squares is similar for both. Therefore this index expresses spatial variation in habitat suitability for the species making up the assemblages (von Euler and Svensson 2001).

Functional diversity was considered through the use of Simpson's diversity index for functional traits, such as foraging behaviour (ground, water, flight), diet type (granivorous, insectivorous, herbivorous), nesting place (ground, short vegetation, holes), or migratory status (resident, trans-Saharian, pre-Saharian). Simpson's diversity index measures the probability that any two individuals picked up at random from a community belong to the same species or category (Simpson 1949), which is given by

$$D = \Sigma\, p_i^2$$

where D is Simpson's index and p_i is the proportion of species i in the community. For computation purposes, the reciprocal of Simpson's index (1/D) is most frequently used (Hill 1973; Krebs 1994). This reciprocal varies from 1 to S, where S is the maximum number of species in the community, or the maximum number of functional categories that can be expected for a given trait. The value of 1/D increases with the number of different species/categories, but it does also with the degree of evenness in their respective proportions (Krebs 1994). Diversity measures that include evenness are robust to undesirable mathematical effects of increasing richness (i.e. diversity cannot decrease when the number of species increases, see Petchey and Gaston 2006), which makes them suitable for comparison across

different assemblages. Therefore, the reciprocal of Simpson's index was used to measure functional diversity in this study.

Table 2. Community indices used to assess the taxonomic, phylogenetic and functional diversity of farmland bird assemblages in the eight European study localities considered. Foraging: diversity of foraging strategies; Nesting: diversity of nesting strategies; Diet: diversity of diet type; Migration: diversity of migration strategies; TD: taxonomic distinctiveness.

Index	Description	Categories	Source
Foraging	Simpson's diversity index for different foraging techniques of individuals in the assemblage.	Ground, Ground probing, Ground/Flight, Water/Ground, Water/Ground Probing, Flight-Scanning, Flight	
Nesting	Simpson's diversity index for different nesting estrategies of individuals in the assemblage.	Ground, Short vegetation, Holes	
Diet	Simpson's diversity index for different diet types of individuals in the assemblage.	Granivorous, Insectivorous, Omnivorous-Granivorous, Omnivorous-Herbivorous, Herbivorous	
Migration	Simpson's diversity index for different migratory status of individuals in the assemblage.	Resident, Trans-saharan, Pre-saharan	Del Hoyo et al. various years
Co-occurrence	Number of survey squares in which two given species co-occur, divided by the number of squares in which either one or the other occur		VonEuler & Svensson 2001
TD	Measurement of taxonomic distinctness of species in the whole data set, averaged per assemblage		Warwick & Clarke 1998; VonEuler & Svensson 2001
Richness	Species richness per assemblage		
Abundance	Individual abundance per assemblage		

Indices used are summarized in Table 2. The list of all species recorded and the category or value assigned to each one in the building of indices can be consulted in Appendix Table 5 of Supplementary Material. Each index was used as a response variable in a General Lineal Model (GLM, type III sum of squares) analysis, using the intensification variables significantly explaining species abundance according to the previous CCA as independent variables. The potential influence of geographical location of study site was considered through the inclusion of a random factor 'study site' in the model. The frequency distribution of each response variable assumed in each modelling procedure varied depending on the particular index being analysed (see Table 2) and, although GLMs are robust to deviations from normality, independent variables were transformed to meet normality requirements when necessary. Given the small number of independent variables in relation with the large sample size available (n= 240: 30 survey plots x 8 study sites), over-fitting was not considered to be a problem (Crawley 2002). An information theory modelling approach was used to select the most parsimonious model for each assemblage index: that including the least number of variables for the lowest value of Akaike's Information Criteria (AIC) in a set of possible models (Burnham and Andersson 2003). Since the final aim was to identify intensification variables significantly influencing indices, an all-effects analysis was performed on each model to test the significance of individual variables. These analyses were performed in STATISTICA 8.0 (Statsoft 2007).

Results

The Canonical Correspondence Analysis performed to identify the fractions of variance explained by intensification variables and geographical location allowed to select a subset of significant variables by means of forward step-wise regression from the initial set of intensification variables considered. These significant variables are highlighted in Table 1. The main aspects of agricultural intensification are taken into account by this set of 11 variables: field-scale management practices (yield, pesticide and nitrogen-fertiliser inputs, frequency of soil disrupting operations), field-scale habitat quality for birds (carabid and weed richness), farm layout (farm size, number of crops, area under agri-environmental schemes) and landscape features (area covered by arable crops and mean field size). All regression models used in variance partitioning were statistically significant (species abundance in relation to intensification variables, $F= 9.85$; $p= 0.002$; species abundance in relation to country, $F= 22.2$; $p= 0.001$; species abundance in relation to intensification including study site as covariable, $F= 4.58$; $p= 0.01$; and species abundance in relation to country with intensification variables as the covariable matrix, $F= 10.53$; $p= 0.002$). Canonical axes resulting from the CCA are shown in the supplementary figure of Appendix Figure 3; both those obtained with intensification variables as predictors, including study site as a covariable matrix, and those obtained with study site as predictor and intensification as covariable. In the first case the 'pure' effect of agricultural intensification on the variation of abundance of the different species between study sites is shown, which corresponds to a 4.27% of the total variance. In the second case, the 'pure' effect of

study site in such variation is described, which explains up to 19.5% of total variance. The combined effect of both groups of variables (intersection) explains 37.81% of total variation, whereas the remaining (unexplained) variance sums up to 38.41 %. In other words, nearly two fifths of variation in farmland bird species abundance can be attributed to a combination of geographic and agricultural intensification factors, while geography alone accounts for another fifth of that variation. The proportion of variation that can be attributed to agricultural intensification alone is much smaller but still significant. Finally, the fraction of variation that cannot be attributed to any of the two factors considered is also nearly two fifths. This variance partitioning is graphically described in Figure 2.

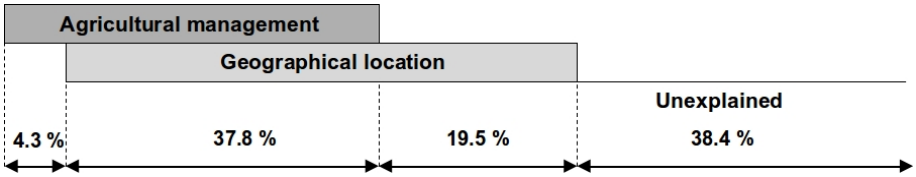


Fig. 2. Variance partitioning in farmland bird abundance across study sites in Europe as obtained in CCA models. Horizontal bars show the percentage of variance explained by agricultural intensification and geographical location. Overlapping sections indicate coincident explained variation.

The results of GLMs analysing the relationships of indices measuring the state of assemblages in terms of taxonomic and functional diversity with agricultural intensification variables are summarized in Table 3. Study site was significant in all models but one (diversity of diet types), reflecting the effect of geographical location on assemblage condition. Diversity of foraging strategies was positively related to weed richness and the surface covered by arable

land, and negatively to farm size. Diversity of nesting strategies showed a positive relationship with weed richness and the amount of nitrogen fertiliser. Diet type diversity was positively related to the amount of nitrogen fertiliser, and negatively to farm size and yield. The diversity of migratory status presented a positive relationship with weed richness and the area of arable crops, while it related negatively to farm size. Both the co-occurrence index and taxonomic distinctiveness were positively related with weed richness and negatively with farm size. Bird species richness was positively related to weed species richness and negatively to farm size. Finally, bird abundance related positively with carabid richness and the number of crops in the farm and the area of arable crops, and negatively to farm size.

Table 3. Intensification variables found to be significant in all-effects GLM analyses for each community index. Asterisks indicate the significant effect of the random factor study site in models.

	Foraging		Nesting		Diet		Migration		Co-occurrence		TD		Richness		Abundance	
R-square	0.24		0.21		0.11		0.33		0.40		0.30		0.48		0.51	
Country	*		*		ns		*		*		*		*		*	
	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE
Carabid richness															1.05	0.5
Weed richness	0.03	0.01	0.04	0.01			0.03	0.01	0.06	0.02	0.11	0.07	0.32	0.12		
Farm Size	-0.04	0.01			-0.27	0.01	-0.03	0.01	-0.08	0.03	-0.30	0.09	-0.54	0.17	-1.67	0.5
Number of crops															1.31	0.4
Yield					-0.05	0.01										
Nitrogen fertiliser			0.05	0.01	0.04	0.01										
Cereal surface	0.03	0.01					0.02	0.01							1.29	0.4

Discussion

Farmland bird assemblage variation across Europe

Our variance partitioning analysis shows that the geographical location of study sites in the European continent alone explains nearly one fifth (19.5%) of total variation in species composition and abundance. The fraction of total variance that can be attributed to variables related with agricultural intensification alone was comparatively smaller (4.3%) but statistically significant (Figure 2). Nevertheless, the intersection of geographical location and agricultural intensification explained a much larger part of variance in species abundance

These results support the idea that large scale bio-geographical gradients still exert a strong influence on community composition across the European continent in spite of the profound landscape transformations and homogenization occurred over the last decades due to agricultural intensification (Robinson and Sutherland 2002; Sanderson et al. 2005). The CCA on the effect of geographical location yielded a marked axis associated to the abundance of steppe bird species (Appendix figure 3a), such as the great (*Otis tarda*, Linnaeus) and little bustards (*Tetrax tetrax*, Linnaeus), the red-legged partridge (*Alectoris rufa*, Linnaeus), the corn bunting (*Emberiza calandra*, Linnaeus), the fan-tailed warbler (*Cisticola juncidis*, Rafinesque) or the crested lark (*Galerida cristata*, Linnaeus), whose distribution in Europe is mainly Mediterranean. In our data set, most observations of these species come from Spain, which highlights the importance of Spanish (and other Mediterranean) cereal

pseudo-steppes in the shaping of large scale biodiversity patterns in Europe. This is consistent with their recognised bio-geographical singularity among European agro-ecosystems (Santos and Suárez 2005).

In relation to the pure effect of agricultural intensification variables on variance partitioning (Appendix figuer 3b), the CCA yielded a group of axes related to landscape structure variables, such as area of arable crops and number of crops, and another group of axes related to field management practices associated to intensification and its results in terms of biodiversity. In fact, these axes seem to define an intensification gradient with diversity of carabids and weeds in one extreme and yield and amount of fertilisers on the opposite. It is interesting to note that the association of some bird species to these gradients is quite consistent with their known ecology in Europe. For example, it is known that species like the great bustard and the Montague's harrier (*Circus pygargus*, Linnaeus) use and select landscapes largely dominated by arable land in western Europe (Morales et al. 2006; Arroyo et al. 2004), as is the preference of crested larks for fallows and other weed-rich habitats (Suárez et al. 2009). However, the relationship of many species to these gradients is difficult to understand without considering the combined effect of both geographical location and agricultural intensification. In this respect, there is an association of most steppe species to farming practices and habitat characteristics frequently found in the extensive cereal farmland of central Spain with weed control through mechanical soil disrupting or ploughing (Appendix figure 3c). In any case, the persistence of the steppe species group in both the combined and geographical-pure effect canonical analyses suggest greater

importance of bio-geographical factors, as compared to agricultural management, in the presence and abundance of these particular species within European farmland bird assemblages.

Agricultural intensification and taxonomic and functional diversity

A series of recent studies have measured the response of farmland bird communities to habitat fragmentation and disturbance at the landscape level (Devictor and Jiguet 2007; Devictor et al. 2008; Devictor and Robert 2009). However, the results presented here are, to our knowledge, the first to describe the effect of variables explicitly measuring agricultural intensification at the field and farm levels on farmland bird taxonomic and functional diversity at European scale.

The variables that more consistently and negatively affect taxonomic and functional diversity are farm size (that is, the total amount of land managed by a single farmer or land-owner) and cereal yield, which are surrogates of farming intensity (Donald et al. 2001; Robinson and Sutherland 2002; Geiger et al. 2010). In the particular case of yield, it has been shown to negatively correlate with species richness in a variety of taxa associated to farmland such as birds, carabids and weeds, as well as with farmland potential for pest control, in a wide range of farming contexts across Europe (Geiger et al. 2010). In the present study, therefore, we show the negative effect of agricultural intensification, not only on farmland bird species richness and abundance, but also on functional diversity aspects such as the diversity of diet types and foraging, nesting and migration strategies. In other words, agricultural intensification negatively affects the functional diversity of farmland bird assemblages in terms

of the different ecological niches comprised by the species assemblage (Von Euler and Svensson 2001; Julliard et al. 2006).

Other functional aspects of the community are also negatively affected by these intensification factors, such as the diversity of species using the same survey plot (measured through the co-occurrence index), or the phylogenetic variety of the assemblage (measured through the taxonomic distinctiveness index). These results show that more intensively farmed areas hold less diverse bird assemblages also at small scale (field or farm scale), and that these assemblages are taxonomically simplified (dominated by phylogenetically closer taxa, see Von Euler and Svensson 2001) in relation to what is found in more extensive sites.

Assemblage functional indices also respond positively to variables related with habitat availability, such as the area of arable crops, and with less intensive farming, such as weed richness (see Kleijn et al., 2009; Geiger et al. 2010). Additionally, weed richness, which is significant in six models, can be interpreted as a measure of food availability, either directly for birds, or via the intermediate consumption by invertebrates. An equivalent interpretation can be given to the strong positive effect of carabid richness on total bird abundance (see Geiger et al. 2010). These results suggest a relevant role of food resources in determining bird assemblage species and functional diversity, which is consistent with general knowledge on community functioning (Begon et al. 1996). In relation to the area occupied by arable crops, it should be recalled that the species considered in this study are all open-country ground-nesting farmland birds (see Potts 1991; Suárez et al. 1997) and thus the use of this

variable as a measure of habitat availability is legitimate and consistent with the results obtained.

Finally, the amount of nitrogen fertilizer had a positive effect on nesting strategy and diet type diversities. In spite of reducing plant richness in crops (Tilman 1993; Kleijn et al. 2009), greater nitrogen inputs may favour global system productivity and the increase in abundance of some plant species, thus contributing to increase habitat carrying capacity for birds in terms of nesting site heterogeneity and availability of more food resources. Besides, and according to the cited authors, the negative effect would be minimal in the more intensified areas.

Between- site differences in taxonomic and functional diversity

Although geographical variation can explain some of the differences in species richness and composition between the European regions included in this study (Rosenzweig 1995; Pianka 1996; Hawkins et al. 2003), their different levels of agricultural intensification are also expected to be related with the ecological condition of their farmland bird assemblages, so that the more intensively cultivated areas should harbor the less taxonomically and functionally diverse assemblages. The statistical significance of the 'study site' factor in almost all models analysing the response of assemblage indices is consistent with the relatively large amount of variance explained by the geographical location of study sites found in the CCA (Figure 2). Globally, the bird assemblage that showed an overall better condition in relation to the community indices considered was the Polish one, which presented the greatest

ground-nesting farmland bird richness and abundance, as well as the highest values of the co-occurrence and taxonomic distinctiveness indices. Also, the Polish assemblage yields the highest values of foraging and migratory status diversity, and the second highest values of diet type and nesting diversity. This suggests that the farmland bird assemblage found in the Polish study site has greater integrity in terms of species, phylogenetic and functional diversity. In spite of its biogeographically singular steppe bird assemblage, the Spanish site does not hold a particularly 'healthy' farmland bird community in terms of species, taxonomic and functional diversity. This is a relevant result since the Spanish study site is a hot spot for steppe birds (Traba et al. 2007) known to host populations of several globally declining species (great and little bustards, lesser kestrel) that are being the target of important conservation actions under the premise that habitat management measures focused on them would have general benefits to the entire farmland bird community. Our results suggest that this assumed umbrella effect would not be operating in our Spanish study site.

Conclusions

Our results show that the composition differences between farmland bird assemblages across our European study sites are explained by geography alone in a notably greater degree than by differences in the level of agricultural intensification between sites, although the largest amount of variance in assemblage composition is explained by the combined effect of both factors. Most of the purely geographical variation is associated to Mediterranean steppe species, which reflects the biogeographical singularity of that assemblage

linked to the cereal pseudo-steppes of the Iberian Peninsula. These results reinforce the need to maintain the still relatively extensive farming in that part of the continent in order to preserve this community and its globally threatened species.

The response of community indices to agricultural intensification factors is consistent with the negative effects of landscape-level disturbance on farmland bird communities found in previous studies, highlighting the relevance of field and farm-scale management on the taxonomic and functional diversity of farmland bird assemblages. In this context, surrogates of intensification like farm size and yield have general negative effects on assemblages, whereas correlates of habitat availability and quality like the extent of arable land and weed richness favour their taxonomic and functional diversity. The analysis of differences between our study sites shows that those with the most taxonomically and functionally diverse bird assemblages (e.g. the Polish one) are those related to less intensive farming practices.

Acknowledgements

We thank the European Science Foundation and the connected national science foundations for funding the presented study through the Eurodiversity AGRIPOPES programme, as well as all collaborating fieldworkers and farmers.

Appendices

Appendix 1. Table 4. Three different criteria were used to define breeding bird territories depending on the species' detectability and breeding behaviour. A: at least two observations of birds displaying territorial behavior at the same spot during different survey rounds; B: one observation of territorial behavior (species unlikely to be present during all the three survey visits or species considered difficult to observe); C: direct evidence of breeding activities.

English name	Scientific name	breeding category
Black-tailed Godwit	*Limosa limosa*	A
Calandra Lark	*Melanocorypha calandra*	A
Corn Bunting	*Miliaria calandra*	A
Corncrake	*Crex crex*	B
Crested Lark	*Galerida cristata*	A
Curlew	*Numenius arquata*	B
Fan-tailed Warbler	*Cisticola juncidis*	A
Gadwall	*Anas strepera*	C
Great Bustard	*Otis tarda*	B
Greylag Goose	*Anser anser*	C
Lapwing	*Vanellus vanellus*	A
Little Bustard	*Tetrax tetrax*	B
Mallard	*Anas platyrhynchos*	C
Montagu's Harrier	*Circus pygargus*	C
Meadow Pipit	*Anthus pratensis*	A
Marsh Harrier	*Circus aeruginosus*	C
Marsh Warbler	*Acrocephalus palustris*	B
Ortolan Bunting	*Emberiza hortulana*	B
Oystercatcher	*Haematopus ostralegus*	A
Wood Sandpiper	*Tringa glareola*	A
Grey Partridge	*Perdix perdix*	B
Pheasant	*Phasianus colchicus*	A
Quail	*Coturnix coturnix*	B
Red-legged Partridge	*Alectoris rufa*	B
Skylark	*Alauda arvensis*	A
Stonechat	*Saxicola torquata*	A
Snipe	*Gallinago gallinago*	A
Short-toed Lark	*Calandrella brachydactyla*	A
Stone-curlew	*Burhinus oedicnemus*	A
Tawny Pipit	*Anthus campestris*	B

Appendix 1. Table 4. Cont.

English name	Scientific name	breeding category
Wheatear	*Oenanthe oenanthe*	A
Whinchat	*Saxicola rubetra*	A
Woodlark	*Lullula arborea*	A
Yellowhammer	*Emberiza citrinella*	A
Yellow Wagtail	*Motacilla flava*	A

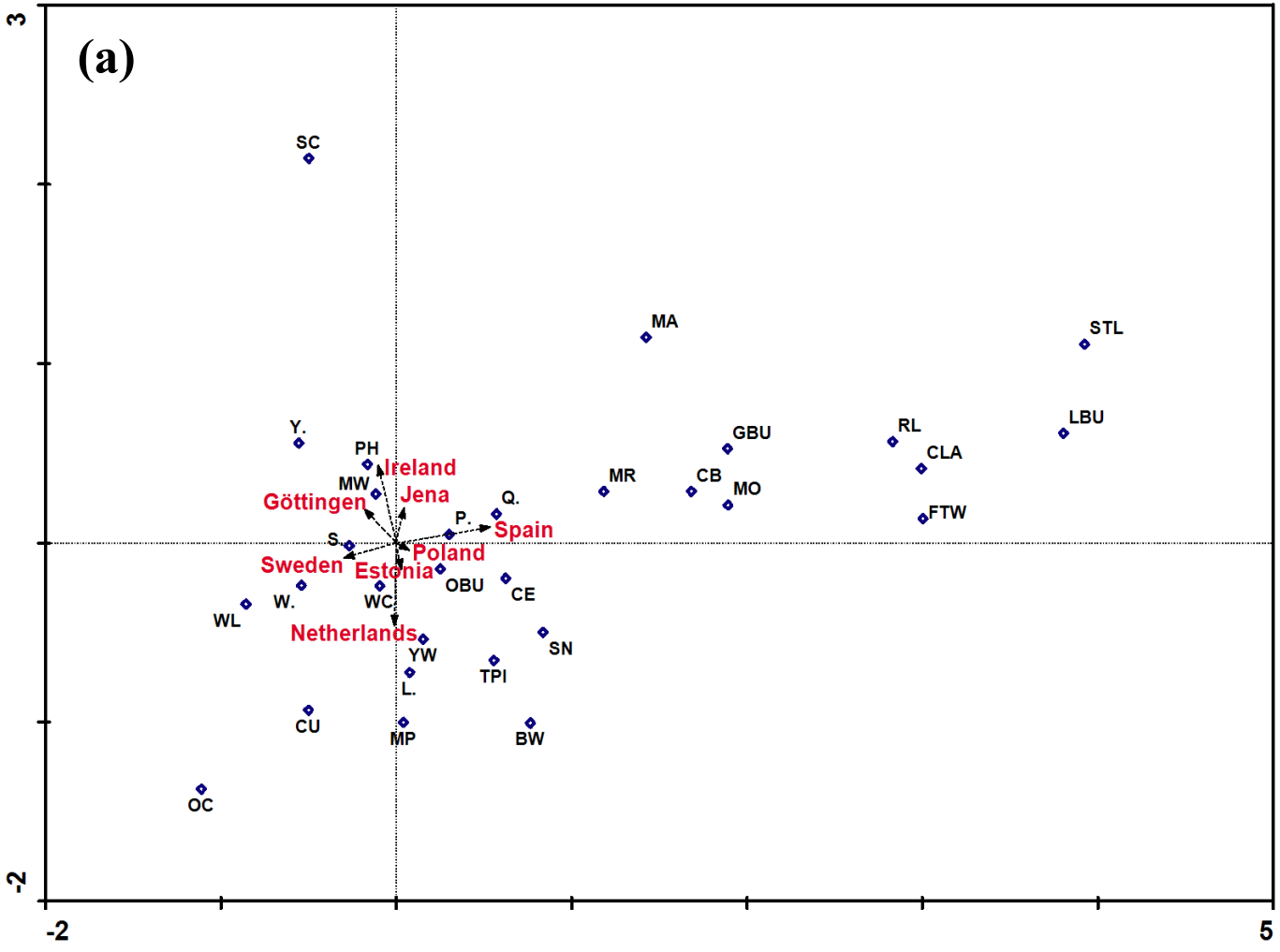
Appendix 2. Table 5. Ground-nesting farmland bird species considered in this study and functional categories used to calculate Simpson's diversity indices for 'Foraging Strategy', 'Nesting Strategy', 'Diet Type' and 'Migration Status'. Information obtained from Cramp and Simmons' *Birds of the Western Paleartic* and Del Hoyo et al. *Handbook of the Birds of the World*.

English Name	Scientific Name	BTO Code	Foraging Strategy	Nesting Strategy	Diet Type	Migration Status
Black-tailed Godwit	*Limosa limosa*	BW	Ground	Ground	Insectivorous	Trans-saharian
Corn Bunting	*Emberiza calandra*	CB	Ground	Ground	Omnivorous/seed-eater	Resident
Corncrake	*Crex crex*	CE	Ground	Ground	Omnivorous/herbivorous	Trans-saharian
Crested Lark	*Galerida cristata*	CLA	Ground	Ground	Omnivorous/seed-eater	Resident
Curlew	*Numenius arquata*	CU	Ground probing	Ground	Insectivorous	Pre-saharian
Fan Tailed Warbler	*Cisticola juncidis*	FTW	Ground/flight	Short veg.	Insectivorous	Resident
Great Bustard	*Otis tarda*	GBU	Ground	Ground	Herbivorous	Resident
Lapwing	*Vanellus vanellus*	L.	Ground	Ground	Insectivorous	Pre-saharian
Little Bustard	*Tetrax tetrax*	LBU	Ground	Ground	Herbivorous	Resident
Mallard	*Anas platyrinchos*	MA	Water/ground	Ground	Omnivorous/herbivorous	Resident
Montagu's Harrier	*Circus pygargus*	MO	Flight-scanning	Ground	Carnivorous	Trans-saharian
Meadow Pipit	*Anthus pratensis*	MP	Ground	Ground	Insectivorous	Pre-saharian
Marsh Harrier	*Circus aeruginosus*	MR	Flight-scanning	Ground	Carnivorous	Pre-saharian
Marsh Warbler	*Acrocephalus palustris*	MW	Flight	Short veg.	Insectivorous	Trans-saharian
Ortolan bunting	*Emberiza hortulana*	OBU	Ground	Ground	Omnivorous/seed-eater	Trans
Oyster Catcher	*Haematopus ostralegus*	OC	Water/ground probing	Ground	Insectivorous	Trans-saharian
Grey Partridge	*Perdix perdix*	P.	Ground	Ground	Herbivorous	Resident
Pheasant	*Phasianus colchicus*	PH	Ground	Ground	Omnivorous/herbivorous	Resident
Quail	*Coturnix coturnix*	Q.	Ground	Ground	Omnivorous/seed-eater	Trans
Red-legged Partridge	*Alectoris rufa*	RL	Ground	Ground	Omnivorous/herbivorous	Resident
Skylark	*Alauda arvensis*	S.	Ground	Ground	Omni-g	Pre-sharian

Appendix 2. Table 5. Cont.

English Name	Scientific Name	BTO Code	Foraging Strategy	Nesting Strategy	Diet Type	Migration Status
Stonechat	*Saxicola torquata*	SC	Ground/flight	Ground	Insectivorous	Pre-saharian
Snipe	*Gallinago gallinago*	SN	Water/ground probing	Ground	Insectivorous	Pre-sahariam
Short-toed Lark	*Calandrella brachydactyla*	STL	Ground	Ground	Seed.eater	Trans-saharian
Tawny Pipit	*Anthus campestris*	TPI	Ground	Ground	Insectivorous	Trans-saharian
Northern Weather	*Oenante oenanthe*	W.	Ground/flight	Holes	Insectivorous	Trans-saharian
Winchat	*Saxicola rubetra*	WC	Ground/flight	Ground	Insectivorous	Trans-saharian
Woodlark	*Lullula arborea*	WL	Ground	Ground	Omni-g	Pre-saharian
Yellowhammer	*Emberiza citrinella*	Y.	Ground	Ground	Omni-g	Pre-saharian
Yellow Wagtail	*Motacilla flava*	YW	Ground/flight	Ground	Insectivorous	Trans-saharian

Appendix 3. Figure 3. Canonical axes resulting from the Canonical Correspondence Analysis (CCA) of farmland bird abundance in relation to (a) study site as predictor and intensification variables as covariables (pure effect of study site), (b) to intensification variables as predictors and study site as covariable (pure effect of intensification), and (c) only to intensification variables as predictors (mixed effect). BW: Black-tailed Godwit, CB: Corn Bunting, CE: Corncrake, CLA: Crested Lark, CU: Curlew, FTW: Fan-Tailed Warbler, GBU: Great Bustard, L: Lapwing., LBU: Little Bustard, MA: Mallard, MO: Montagu's Harrier, MP: Meadow Pipit, MR: Marsh Harrier, MW: Marsh Warbler, OBU: Ortolan Bunting, OC: Oyster Catcher, P.: Grey Partridge, PH: Pheasant, Q.: Quail, RL: Red-legged Partridge, S.: Skylark, SC: Stonechat, SN: Snipe, STL: Short-toed Lark, TPI: Tawny Pipit, W.: Northern Weather, WC: Winchat, WL: Woodlark, Y.: Yellowhammer, YW: Yellow Wagtail. AES: Agri-environmental schemes, CarabRich: Carabid richness, FarmSize: Farm size, Insectic: Insecticide, MeanFieldSize: Mean field size in landscape, Nfert: N fertiliser, NrCrops: Number of crops, PercentArable: Cereal surface in landscape, SoilDisrupt: Soil disrupting, WeedRich: Weed richness, Yield: Yield.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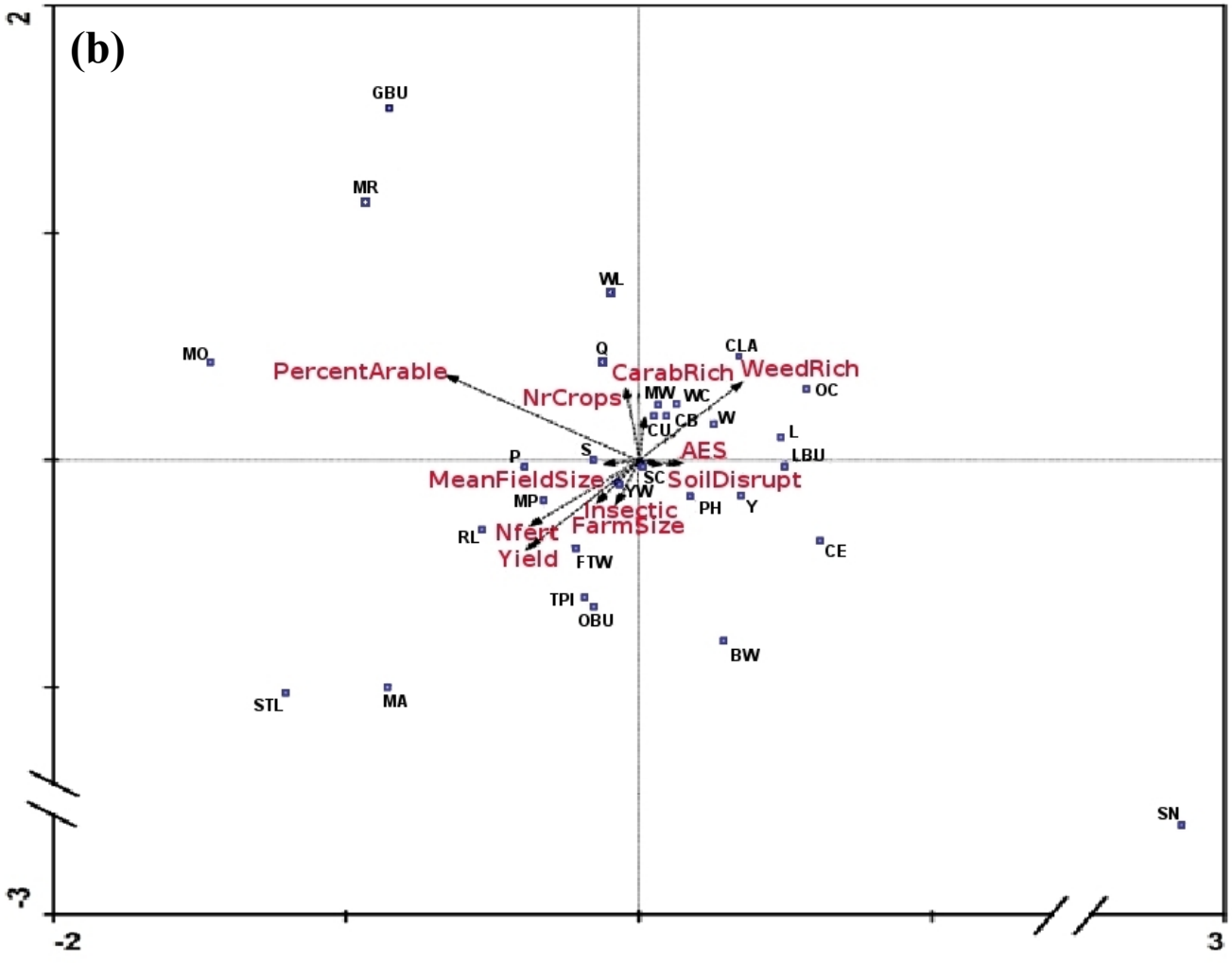
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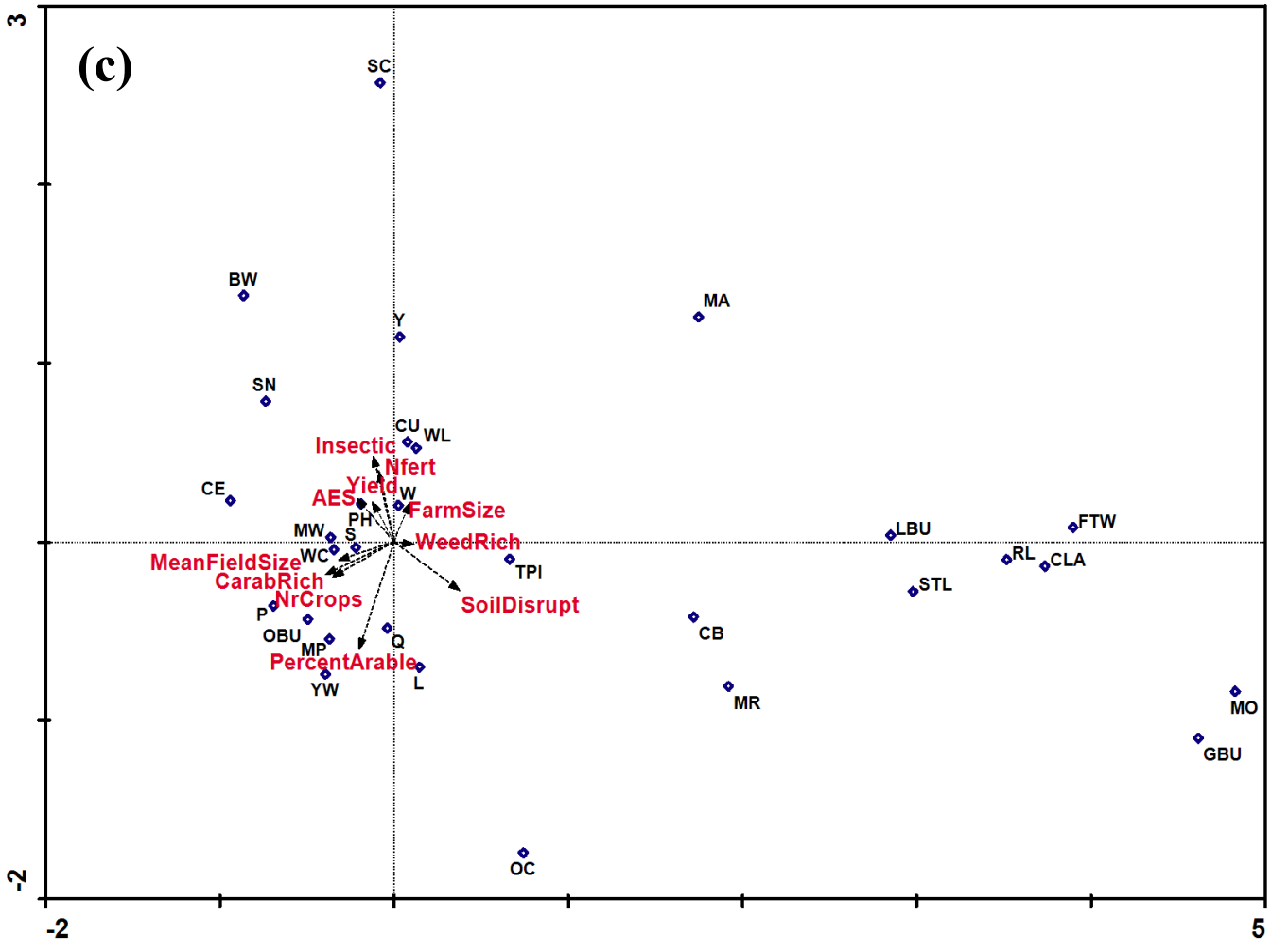
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CAPÍTULO III

Respuesta de las aves especialistas de medios agrarios a la intensificación agraria en Europa: factores de gestión a escala de campo y paisaje.

Este capítulo reproduce íntegro el siguiente manuscrito:
Guerrero,I.; Morales,M.B.; Oñate,J.J.; Geiger,F.; Berendse,F.; de Snoo,G.; Eggers,S.; Pärt,T.; Bengtsson,J.; Clement,L.W.; Weisser,W.W.; Olszewski,A.; Ceryngier,P.; Hawro,V.; Liira,J.; Aavik,T.; Fischer,C.; Flohre,A.; Thies,C. & Tscharntke,T. (2012) Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. *Biological Conservation,* 152: 74-80

Resumen

La intensificación agraria es considerada la principal causa de los dramáticos declives experimentados en las últimas décadas por las poblaciones de aves ligadas a los medios agrarios en Europa. Identificar los factores de intensificación específicos responsables de estas tendencias resulta vital para la conservación en los sitemas agrarios europeos.

Investigamos la respuesta de aves especialistas de medios agrarios al proceso de intensificación agraria en seis países europeos cubriendo un gradiente biogeográfico y de intensificación. Mediante un ACP, consideramos dos grupos de factores de intensificación agraria: uno relacionado con la gestión a nivel de campo de cultivo, y otro con la modificación del paisaje, tratando de discriminar la importancia relativa de los efectos de estos dos componentes de la intensificación agraria. El análisis de partición de la variación mostró que los factores de paisaje explican la mayor parte de la variación de las densidades de individuos y territorios de aves especialistas de medios agrarios, y también de las densidades de individuos de Alondra común. Los factores relacionados con la gestión a nivel de campo de cultivo fueron más importantes a la hora de explicar la densidad de territorios de Alondra. Nuestros resultados sugieren que, en general, las densidades de aves especialistas son mayores en paisajes simples dominados por la agricultura, pero con campos pequeños y mayor diversidad de cultivos por explotación. Además, los rendimientos agrarios elevados se relacionaron negativamente con estas densidades.

Concluimos que, en relación a la conservación de las aves ligadas a medios agrarios, mientras las medidas de gestión a escala de paisaje podrían ejercer un efecto muy positivo en las densidades de individuos, las medidas a nivel de gestión de campos de cultivo son también relevantes, en especial para los individuos reproductores, por lo que potencialmente podrían influir en la persistencia de sus poblaciones.

Abstract

European farmland bird populations have decreased dramatically in recent decades and agricultural intensification has been identified as the main cause contributing to these declines. Identifying which specific intensification pressures are driving those population trends seems vital for bird conservation in European farmland.

We investigated the response of ground-nesting farmland birds to the multivariate process of agricultural intensification in six European countries covering a bio-geographical and intensification gradient. Supported by PCA analysis, two groups of factors, related to field management and landscape modification, were considered, seeking to discriminate the relative importance of the effects of these main intensification components.

Variance partition analysis showed that landscape factors accounted for most of the variation of ground-nesting farmland bird individual and breeding pair densities, as well as Skylark (i.e. our single model species) individual densities. In the case of Skylark breeders, field factors were found to be more important to explain their density. Our results suggest that in general farmland bird densities as well as Skylark densities are higher in simple landscapes dominated by agriculture, but with smaller fields and more different crops on the farms. In addition, high yields were negatively related to bird densities.

We conclude that while management actions aimed at farmland bird conservation taken at landscape level may exert a strong positive effect on overall bird densities, those taken at field level are also relevant, particularly for breeders and, therefore, may potentially influence the persistence of these species' populations.

Keywords: *Alauda arvensis*, breeding territories, conservation, Skylark, yield, winter cereals.

Introduction

Farming shapes the majority of European landscapes. Farmland covers 43% of the surface area of the European Union (EU-27) and hosts 50 % of all European bird species (Pain and Pienkowski, 1997). Among European agricultural systems, cereal crops comprise about 21 % of European land cover (33.81 million ha or third of the total European area devoted to agriculture, EUROSTAT, 2010) and therefore they are directly used by a significant proportion of bird species, including a number of endemic and threatened ones, which are the main targets of a wide range of biodiversity conservation measures (European Commission, 2003).

In recent decades, however, European farmland bird populations have decreased to a worrisome extent, showing stronger declines than those suffered by bird communities in other habitats (Gregory et al., 2005). Agricultural intensification has been identified as the main cause contributing to these declines, affecting the suitability and availability of foraging and breeding habitats through changes in management factors such as increased input applications and loss of ecological heterogeneity at different scales (Benton et al., 2003; Donald et al., 2001a; Robinson and Sutherland, 2002). Whereas this causality is well documented, the mechanisms by which the intensification process affects bird populations remain less understood. Diverse agricultural management factors have changed simultaneously, turning agricultural intensification into a multivariate process whose components are difficult to disentangle (Chamberlain et al., 2000). Thus, farmland bird populations respond to a whole suite of

changes in management factors carried out by farmers at individual farm level but acting at different spatial scales and in different dimensions, from landscape structure modifications to crop management actions at field level (Concepción and Díaz, 2010; Firbank et al., 2008).

In order to reverse these population trends, identifying which are the specific driving pressures seems vital for farmland bird conservation in Europe. Establishing the relative importance of intensification components acting at different spatial scales (i.e. field and landscape) should help to better target conservation measures, such as agri-environmental schemes, and support the policy mechanisms required for their implementation (Concepción and Díaz., 2010). It is known that the most effective conservation measures, in intensively farmed agricultural landscapes, are those minimizing the impact of intensification on the species' reproductive performance (Benton et al., 2003; Casas and Viñuela, 2010; Morris et al., 2005), although in extensive farmlands certain landscape changes associated with intensification may have positive effects on species richness and abundance (Tscharntke et al. 2005; Wretenberg et al. 2007, 2010). Consequently, assessing the effects of intensification on farmland bird breeding activities should help to improve the efficiency of measures aimed at reversing their negative population trends.

We investigate the response of ground-nesting farmland birds to the multivariate process of agricultural intensification in six European countries covering a north-south, and an east-west bio-geographical gradient. The study is focused on birds using cereal fields, either for foraging or nesting activities, so that the impact of management

intensification of this important habitat across Europe can be assessed at both local (i.e. field) and landscape spatial levels in order to potentially produce more concrete conservation recommendations. More precisely, we analyse the specific impact of two main groups of intensification factors, on the density of individuals and breeding territories of farmland birds: those related to crop management at field level, and those related to landscape modifying actions. We examine, as well, the contribution of particular management factors within those groups in explaining bird density responses. This approach is further applied to the particular case of the Skylark (*Alauda arvensis*), a cereal farmland specialist nesting on the ground and depending on insect availability and adequate vegetation structure (not too dense and not too high to allow nesting and foraging, Donald, 2004, Eraud and Boutin, 2002). This species, formerly distributed throughout Europe, is currently undergoing an alarming decline in many countries (Donald et al. 2001b).

Methods

Study Area

Bird surveys were carried out in seven regions located in six European countries: Sweden, Poland, the Netherlands, Germany (two areas, based on their contrasted characteristics derived from different land use history: close to Göttingen and Jena), Estonia, and Spain (Figure 1). Each area was between 30x30 and 50x50 km^2 in size. A set of 30 arable farms (defined as a portion of land belonging to a single owner) were selected per area, reflecting an intensification gradient within each study area using the averaged cereal yield from the

previous five years as a proxy for agricultural intensification. Farms were selected so that cereal yield and landscape composition were uncorrelated within a study area.

Figure 1. Location of the study regions in 1. Estonia, 2. Germany (Göttingen), 3. Germany (Jena), 4. the Netherlands, 5. Poland, 6. Spain and 7. Sweden.

Bird surveys

Bird surveys were conducted on the biggest cereal field available per farm. The crop on most focal fields was winter wheat (82 %), the

major cereal crop in Europe, but barley and spring wheat were also included. All surveyed fields were at least 1 km apart.

Surveys were performed during spring and summer 2007, starting according to local information on the phenology of breeding birds, and repeated two more times at intervals of three weeks. Surveys took place between one hour after dawn and until noon, but only if it was not windy, cloudy, or rainy, and were conducted by slowly walking the entire census area, so that each spot was no further than 100 m from the surveyor's route. This is a modified version of the British Trust for Ornithology Common Bird Census protocol (Bibby et al. 1992).

Breeding bird territories were determined for ground-nesting farmland birds, which can, therefore, be considered as farmland specialists, (see Table 1 for a list of considered species) using the combined results of the three survey rounds. Three different criteria were used to define breeding bird territories, depending on the species' detectability and breeding behaviour (Table 1). To meet the criteria for assigning a breeding territory, species of category A had to be observed at least twice displaying territorial behaviour (foraging, calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds. Category B comprised species unlikely to be present during all the three survey visits because of their migration behaviour (e.g., long-distance migrants arriving relatively late) and species considered difficult to observe. For this category, only one observation of territorial behaviour was required. For category C species, direct evidence of breeding activities was required.

Table 1. Farmland bird species detected in the surveys. Species marked with asterisks were considered breeding on focal fields. Categories assigned to define breeding depend on the species' detectability and breeding behaviour. Category A requires at least two observations of birds displaying territorial behaviour at the same spot during different survey rounds. Category B requires one observation of territorial behaviour (species unlikely to be present during all the three survey visits or species considered difficult to observe). Category C requires direct evidence of breeding activities.

Scientific Name	English Name	Cat.
Acrocephalus palustris	Marsh Warbler	B*
Alauda arvensis	Skylark	A*
Alectoris rufa	Red-legged Partridge	B*
Anas platyrhynchos	Mallard	C
Anser anser	Greylag Goose	C
Anthus campestris	Tawny Pipit	B
Anthus pratensis	Meadow Pipit	A*
Burhinus oedicnemus	Stone-curlew	B
Calandrella brachydactyla	Short-toed Lark	A*
Circus aeruginosus	Marsh Harrier	C
Circus cyaneus	Hen Harrier	C
Circus pygargus	Montagu's Harrier	C
Cisticola juncidis	Fan-tailed Warbler	A*
Coturnix coturnix	Quail	B*
Crex crex	Corncrake	B*
Emberiza citrinella	Yellowhammer	A*
Emberiza hortulana	Ortolan Bunting	B
Galerida cristata	Crested Lark	A*
Gallinago gallinago	Snipe	A
Haematopus ostralegus	Oystercatcher	A
Lullula arborea	Woodlark	A*
Miliaria calandra	Corn Bunting	A*
Motacilla flava	Yellow Wagtail	A*
Oenanthe oenanthe	Wheatear	A*
Otis tarda	Great Bustard	B*
Perdix perdix	Grey Partridge	B*
Phasianus colchicus	Pheasant	A*
Saxicola rubetra	Whinchat	A*
Tetrax tetrax	Little Bustard	B
Vanellus vanellus	Lapwing	A*

Agricultural intensification data

Information about yield and farming practices during the sampling year (number of crops per farm, sowing density, pesticides and fertilizers use, ploughing and mechanical weed control regime; see Table 2) was collected by means of a questionnaire sent out to all participating farmers.

Table 2. Agricultural intensification factors used as explanatory variables in variance partitioning analyses.

	Factor	Description	Mean ± SD
Landscape intensification factors	Field Size	Focal Field Size (ha).	13.66±14.86
	Mean Field Size (MFS)	Mean arable field size inside a circle radius 500 m centered on the focal field (ha).	19.19± 31.45
	Land use diversity (LUDiv)	Shannon index (H') of land use categories inside a circle radius 500 m centered on the focal field.	0.54±0.41
	Number of Crops (NrCrops)	Number of different crops cultivated in study farm.	4.96±2.86
Field intensification factors	Yield	Cereal grain obtained from focal field (ton ha^{-1}).	5180.1±2166.6
	Sowing Density (SowDens)	Density of seed sown in focal field (kg ha^{-1}).	197.08±48.22
	Soil disrupting operations (Disrpt)	Number of soil disrupting operations performed with machinery to control weeds.	0.92±1.47
	Inorganic fertilizers (InFert)	Total amount of inorganic fertilizers applied on focal field (kg ha^{-1}).	140.75±120.60
	Herbicides (Herb)	Number of herbicide applications on focal field.	1.21±1.21
	Insecticides (Insect)	Number of insecticide applications on focal field.	1.17±1.72

Two characterizing landscape variables were estimated from digital maps, using Patch Analyst 3.12 extension to the Geographic Information System software ArcView (Rempel et al, 1999), within circles with a radius of 500 m around the centre of each field: mean arable field size (considering the actual size of the field) and Shannon land use diversity index. To estimate land use diversity the following land use classes were used (definitions according to Büttner et al., 2000): continuous urban fabrics, discontinuous urban fabrics, cultivated arable lands, fallow lands under rotation systems, permanent crops, pastures, forests, transitional woodland-scrub and water.

Statistical analyses

Two response variables measuring density of ground-nesting farmland birds were calculated: the maximum density of individuals observed over the three sampling rounds, and the density of breeding territories. Both were calculated for all species defined as ground-nesting farmland species combined, and for the Skylark (*Alauda arvensis*), the most abundant species in the sampling areas, except for the Spanish study area, where this species does not breed.

In the analyses, agricultural intensification factors were divided into two components (see Table 2). The division of agricultural intensification in these two categoriesis further supported by the structure of our data. The explanatory variables were associated to two PCA axes describing a gradient in field management intensification (PC1) and a gradient in landscape simplification (PC2), which explained 31.5 % and 21.3 % of variance, respectively (Table 3).

Table 3. Principal Component loadings for agricultural intensification variables, and explained variance. Variables with loadings over 0.5 are shown in bold.

	PCA1	PCA2
Field Size	0.156	**0.691**
MFS	0.104	**0.887**
LUDiv	-0.238	**-0.659**
Nr.Crops	0.054	**0.573**
Yield	**0.772**	0.220
SowDens	-0.003	-0.055
Disrpt	**-0.670**	-0.068
InFert	**0.836**	0.084
Herb	**0.838**	0.051
Insect	**0.780**	0.193
Expl.Var	31.50%	21.30%

For all analysis, response variables and heavily skewed explanatory variables were log-transformed (this transformation was not needed for Yield and Sowing density). All factors were standardized according to $(x - \mu) / \sigma$, with x = measurement, μ = mean and σ = standard deviation, to enable comparison of the magnitude of their effects. Intensification variables were checked for correlations, and several factors showed significant ($p < 0.05$) inter-correlations, although the Pearson correlation coefficients were never > 0.7. Nevertheless, the applied hierarchical partitioning procedure helps to alleviate problems derived from multi-collinearity by comparing simultaneously all possible models from a set of predictors to assess the average contribution of each variable to the variance (Chevan and Sutherland, 1991; Mac Nally, 2000).

Since our goal was to investigate which, and to what extent, agricultural intensification components may influence ground-nesting farmland bird numbers, rather than to find single predictive models, we used general linear models, with normal error distribution and identity link function, where the additive effects of agricultural intensification components on the numbers of farmland birds in cereal fields were examined. We fitted the models for each response variable including study area as fixed effects.

Variance partitioning analysis (Anderson and Gribble, 1998; Carrete et al., 2007) was used to decompose variation in bird density and breeding territories among three groups of predictors: landscape modification factors, field management factors and study area. Assuming that the R^2 of a linear model is a good measure of the variability in the dataset explained by the included variables, we calculated R^2 for eight variation fractions: (a) pure effect of the landscape intensification component; (b) pure effect of the field intensification component; (c) pure effect of study area; and shared effects of (d) the landscape and field intensification components; (e) the field intensification component and study area; (f) the landscape intensification component and study area; (g) the three groups of explanatory variables; and finally unexplained variation. Subsequently, fractions (*a*) to (*g*) were calculated by solving simple equation systems.

Next, we identified, within each intensification component (i.e. Landscape and Field management) those predictors most likely to influence variation in the dependent variables. To that end, we fitted two separate models, one per component, including all corresponding

predictors, and quantified their independent relative importance and effect using the hierarchical partitioning procedure (Chevan & Sutherland, 1991; Grömping, 2006).

All analyses were performed with the R package *relaimpo* (Grömping, 2006). Note, that the term 'effect' is used for statistical association and does not necessarily mean causality between two variables.

Results

Farmland bird densities

A total of 30 ground nesting farmland bird species were detected in the surveys, 19 of which were considered to be breeding on sampled focal fields (Table 1). The most common species were the Skylark (*Alauda arvensis,* present in 112 of the 180 sampled fields, breeding in 108), doubling the abundance of the next most common species, the Yellow wagtail (*Motacilla flava*). Figure 2 shows the averaged figures of all four density measures for each study area.

Variance partitioning

Together, the three groups of independent variables explained 21 % of the total variation of farmland bird density in the data set. The percentage of explained variation increased to 41 % when the response variable was the density of breeding territories. The summed (pure and combined) effects of landscape related factors accounted for 14 % of the variation of farmland bird density in the data set and for 20 % of variation of breeding territories density. The summed effects of the field management component accounted for 3 % of the total explained

variation of individual density, and rose to 13 % for breeding territory density. Finally, the pure and shared effects of study area accounted for 10 % and 28 % of the total variation in individual density and territory density, respectively (Figure 3a,b).

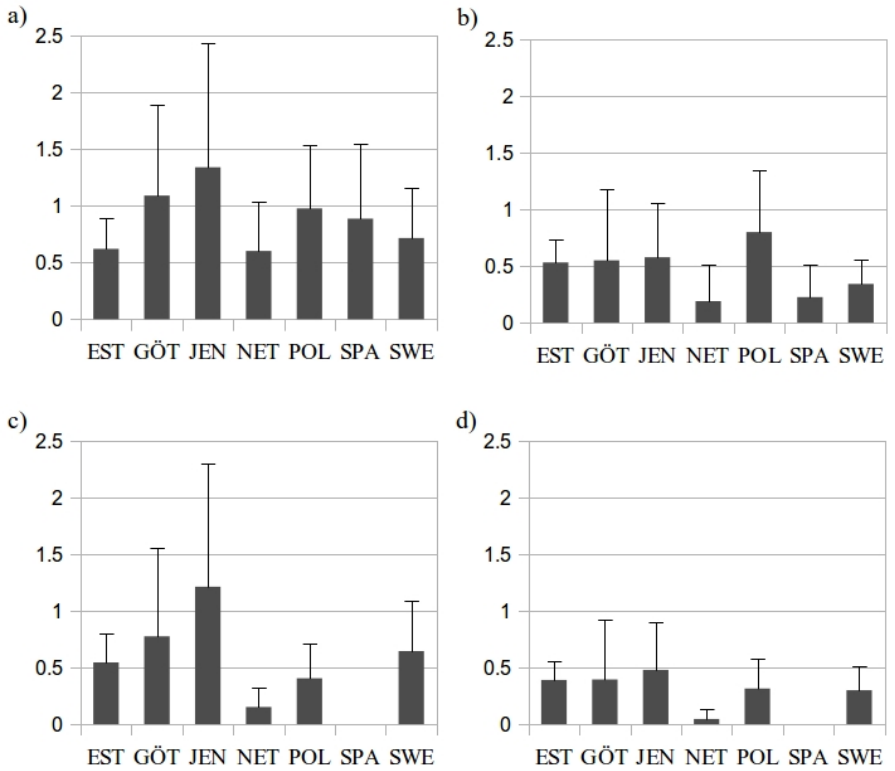

Figure 2. Graphs showing the averaged figures of all four density measures for each study area: a) Farmland bird density, b) Breeding territory density, c) Skylark individual density and d) Skylark territory density.

Regarding the Skylark, the three groups of explanatory variables together accounted for 59 % of the variation in density of individuals, decreasing to 43 % in the case of breeding territory density. Landscape intensification factors (pure and shared effects) explained 23 % of total individual density variation and 11 % of the variation in density of breeding territories. Around 13 % of the variation of Skylark

individual density was explained by the pure and shared effects of the field management component, while this figure rose to 18 % of the total variation of Skylark breeding territories. The pure and shared effects of Study area accounted for 44 % and 31 % of the total variation in the analyses of Skylark individual density and breeding territory density, respectively (Figure 3c, d).

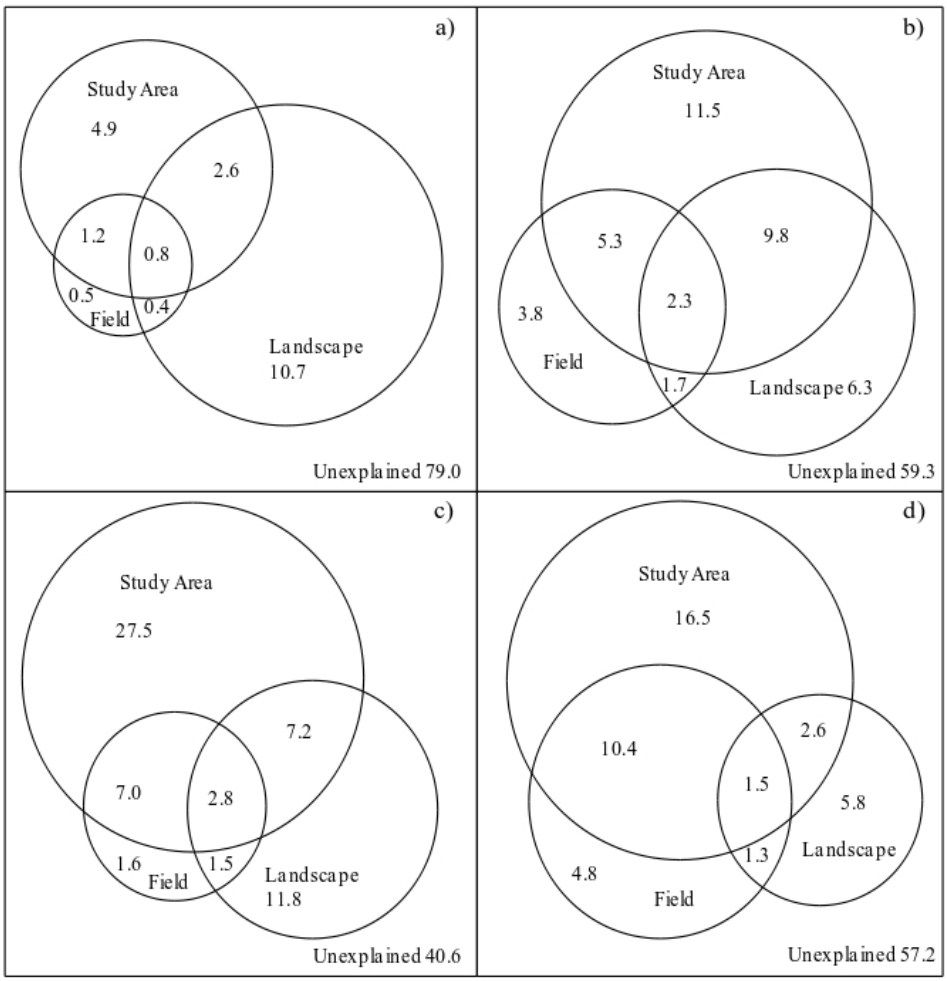

Figure 3. Results of variance partitioning analysis for a) Farmland bird density, b) Breeding territory density, c) Skylark individual density and d) Skylark territory density.

Regarding the particular contribution of factors within the landscape component, land use diversity and focal field size were the main contributors to explain variance in the case of individual farmland bird density, both with negative effect (see Figure 4a), whereas surrounding mean field size, with negative effect, and number of crops, with positive effect, accounted for more variance in the case of breeding territory density (Figure 4b). For the single model species (i.e. Skylark), land use diversity, again, accounted for an important fraction of individual density variance within the landscape group, and surrounding mean agricultural field size was a main contributor explaining both individual and territory densities. These two factors have a negative effect on the response variable (see Figure 4c,d). Regarding the relative importance of factors at field level, the main contributor explaining variance for all four response variables was yield, which has a negative effect (Figure 5).

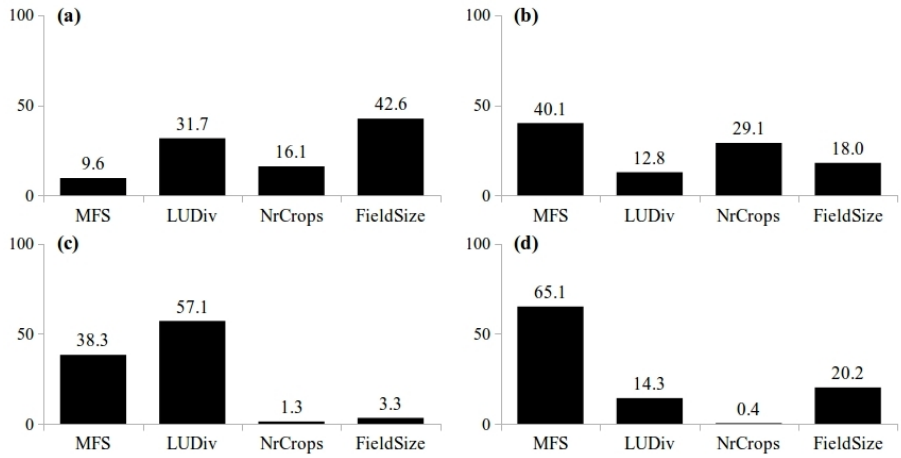

Figure 4. Results of hierarchical partitioning analysis in landscape agricultural intensification component. Average coefficients of main contributors for fitted full models for a) Farmland bird density: FieldSize -0.045, LUDiv -0.22; b) Breeding territory density: MFS -0.012, Nr.Crops 0.026; c) Skylark individual density: MFS -0.0005, LUDiv -0.011; and d) Skylark territory density: MFS -0.008, FieldSize -0.023.

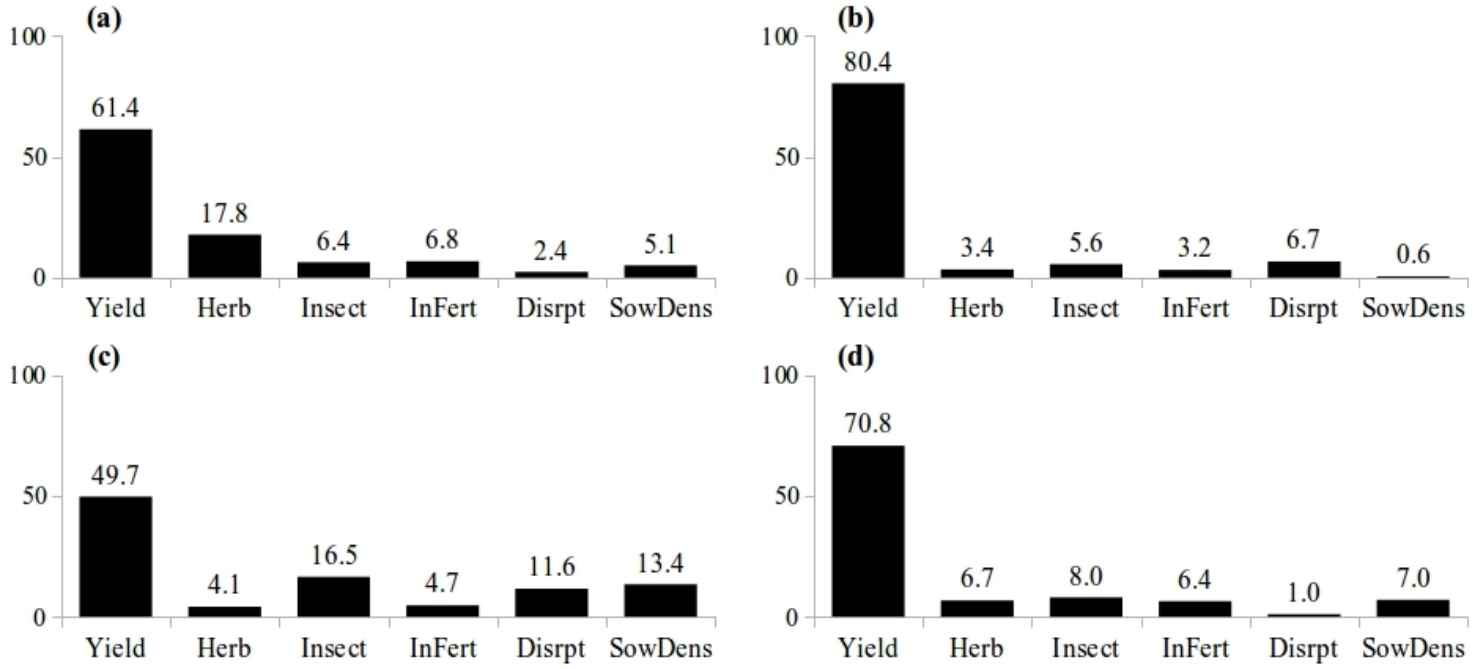

Figure 5. Results of hierarchical partitioning analysis in field management agricultural intensification component. Average coefficients of main contributor, Yield, for fitted full models for a) Farmland bird density: -0.006, b) Breeding territory density: -0.03, c) Skylark individual density: -0.023 and d) Skylark territory density: -0.012.

Discussion

Considering the wide geographical range of this study (comprising large scale climatic gradients, north to south and continental to oceanic, and different socio-economical histories), the importance of the study area in all analyses is not surprising. This suggests, on the one hand, that large scale environmental gradients influence both total ground nesting farmland bird and Skylark densities, similar to what was found for diversity by Guerrero et al.(2011). Nevertheless, the effect of study area has been controlled for in the analysis in order to assess the relative importance for breeding farmland birds of the two main components of intensification. On the other hand, the variation explained by the shared fractions of study area and both agricultural intensification components, suggests that changes in the structure and composition of farmland bird communities have occurred at different rates in different European countries. These results are consistent with the fact that variation in agricultural intensity across Europe has been driven by factors such as different political systems, resulting in particular agrosystem characteristics in our study areas (Donald et al., 2001a, Robinson and Sutherland, 2002; Sanderson et al., 2005).

Agricultural intensification has resulted in a range of different variables influencing organisms' responses at different scales (Chamberlain et al., 2000). The PCA axes represented in Table 3 support this view, showing independent intensification gradients acting simultaneously (Firbank et al., 2008; Persson et al., 2010). In that respect, simplification of landscape structure and composition is known to critically affect farmland bird populations (Heikkinen et al.,

2004; Piha et al., 2007; Wretenberg et al., 2010). Not only the quality of suitable arable habitats, but also their extent, have been identified as major determinants of farmland bird abundance (Connor et al., 2000; Robinson et al., 2001). The negative influence of land use diversity (as an indirect measure of available arable land at the study areas) on the individual density of both all farmland specialists and Skylarks found in this study suggests that many farmland birds are dependent on farmland *per se*.

Additionally, our results support the conclusion that agrosystem simplification associated with agricultural intensification, represented by decreasing number of crops and increasing arable field size, reduces the availability of limiting resources for birds, particularly for breeding pairs (Benton et al., 2003; Vickery et al., 2009; Wilson et al., 2005). A more uniform landscape structure, with large agricultural fields, results in the loss of field margins which has been reported to negatively influence farmland bird populations. Margins provide valuable resources, such as food, refuge or nesting sites (Wilson et al., 1999, Piha et al., 2007). Moreover, increasing field size is related to local management intensity (Persson et al. 2010) and it is known to strongly affect the density of breeding territories of sensible species, such as the Skylark, as this species selects smaller fields for nesting (Eraud and Boutin, 2002).

The impact of field management factors on farmland ground-nesting birds has historically been considered less clear. The wide-ranging nature of these species makes it difficult to link population responses with specific intensification factors acting at ground level (Gregory el al. 2005). Several authors report small

effects of field factors on farmland specialist populations (e.g. Kragten and Snoo, 2008), most of which show a significant dependence on landscape characteristics (e.g. Tscharntke el al., 2005). In other cases, the effects are considered species-specific, identifying some species that are more affected than others by farming practices at the field level (e.g. Eggers et al. 2011; Siriwardena et al., 2000). Our results, however, suggest that the impact depends as well on the use that birds make of the field: the explanatory importance of field management factors increased when breeding territories were analysed, both for all ground nesting birds and for the Skylark. This supports the idea that ground-nesting individuals are more sensitive to farming practices at field scale (Bas et al., 2009; Eggers et al., 2011). In this line of evidence, yield, as a proxy of farming intensification at field scale (Geiger et al., 2010), seems to reflect general effects of intensive crop production on breeding territory densities, both for all species and the Skylark.

In conclusion, while optimum landscape structure and habitat extent are of great importance to preserve ground-nesting farmland bird populations, their recovery in intensively farmed agricultural landscapes might be compromised by the intensive management of cereal fields, which are in fact one of the main breeding habitat for these species throughout Europe. This is particularly evident for open habitat, ground-nesting specialists, such as the Skylark, as these species are currently suffering widespread severe declines.

This study supports the reported influence of landscape structure over farmland bird populations (e.g. Wretenberg et al., 2010). The effectiveness of conservation measures, such as European Union's

agri-environment schemes, has been shown to be moderated by this landscape influence (Concepción et al. 2008). Therefore, crop management measures resulting in landscape-level improvements must be considered when implementing conservation policies, especially in intensive farmland plains (Wretenberg et al., 2007). Nevertheless, our results corroborate, as well, the importance of field level extensification measures (e.g. lower inputs, reduced soil mechanical disrupting, etc.), that should be encouraged in order to reverse farmland bird declines, guaranteeing suitable nesting habitats, in such agricultural landscapes.

Acknowledgements

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CAPÍTULO IV

Asociación interespecífica y uso del hábitat en una comunidad de paseriformes.

Este capítulo reproduce íntegro el siguiente manuscrito:

Morales,M.B.; Guerero,I.; Oñate,J.J. & Meléndez,L. (2012) Inter-specific association and habitat use in farmland passerine assamblage. *Ecological Research,* 27: 691-700

Resumen

En este artículo, se estudió el patrón de asociación interespecífica de territorios de cría en un ensamblado de aves paseriformes en un área de cultivo cerealista del centro de España y se evaluó el papel de la presencia de heteroespecíficos en los patrones de uso de hábitat de distintas especies. Los territorios de estas aves mostraron un patrón de agregación espacial interespecífica. También se estudió la variación en la abundancia de las tres especies más abundantes: el Triguero, el Buitrón y la Cogujada común. Los territorios de Cogujada y Buitrón resultaron más abundantes en lugares con presencia de territorios de Triguero y viceversa, mientras que sus respectivas abundancias no variaron con la presencia de otras especies. Utilizando variables de gestión agraria y composición de paisaje, se analizaron las relaciones entre el hábitat agrario y los territorios de cada especie mediante árboles de regresión. Mientras que el Triguero mostró un marcado patrón de uso de hábitat, la Cogujada y el Buitrón se mostraron un uso más generalista. La presencia de Triguero se relacionó negativamente con relacionadas con la intensificación agraria como el tamaño de parcela o el porcentaje de cobertura de cultivos. De forma similar, la presencia de Cogujada se relacionó negativamente con zonas de alto rendimiento agrario. Sin embargo, cuando la presencia de territorios hetero-específicos se consideró, la presencia de territorios de Triguero fue la variable más influyente en la presencia de territorios de Buitrón y la segunda más importante en el caso de la Cogujada. Estos resultado sugieren que la atracción interespecífica podría jugar cierto papel en la formación de los ensamblados de aves ligadas a los medios agrarios, a la vez que aportan evidencia del efecto nocivo de la intensificación agraria a nivel de comunidades biológicas.

Abstract

We studied the pattern of inter-specific association of breeding territories in a passerine assemblage of dry cereal farmland in central Spain and evaluated the role of the presence of heterospecifics in the habitat use patterns exhibited by different species. Bird territories showed a non-random inter-specific spatial aggregation pattern. We studied territory abundance variation in the three more abundant species, the corn bunting, the crested lark, and the fan-tailed warbler. Crested lark and fan-tailed warbler territories were more abundant in plots where corn bunting territories were present and vice versa, while their respective abundances did not vary with breeding presence of the other species. We used landscape and agricultural management variables to analyse the relationships between habitat and each species' breeding territories by means of classification trees. While the corn bunting showed a marked pattern of nesting habitat use, the crested lark and the fan-tailed warbler exhibited a much more generalist one. Corn Bunting presence was negatively affected by intensification-related variables, such as field size and percent cover of cereal crops. Similarly, presence of crested larks was negatively related to high yielding areas. However, when presence of hetero-specific territories was considered, presence of corn bunting territories was the most important variable explaining occurrence of breeding fan-tailed warblers, and the second most important in the case of the crested lark. These results suggest that inter-specific attraction could play a role in the formation of farmland bird assemblages, while adding further evidence on the detrimental effect of agricultural intensification at the community level.

Keywords: Agricultural intensification, classification trees, corn bunting, crested lark, fan-tailed warbler, habitat use, Spain.

Introduction

The coexistence of different species in ecological guilds can be allowed by niche contraction to avoid inter-specific competition (McArthur 1958; Gotelli and McCabe, 2008). However, coexistence can also arise from the overlapping habitat preferences of different species which meet in a common habitat (Rosenzweig 1981; Morris 1999). In fact, inter-specific relationships and habitat selection are two interacting ecological processes involved in community assemblage: habitat selection may influence the patterns of community assemblage, but also the interactions between species frequently impose constraints on their habitat selection patterns (Rosenzweig 1981; Morris 1999). The role of negative species interactions in habitat selection has been extensively studied (Robinson and Terborgh 1995; Clark and Schluter 1999; Verdolin 2006; Roberts and Liebgold 2008), but also that of positive ones (those favouring species associations) has received attention (but see Slagsvold 1980; Terborhg, 1990; Forsman et al. 2002; Sridhar et al. 2009). Inter-specific association for breeding has been described in many colonial bird species, where larger numbers of breeding pairs allow earlier detection of predators and more efficient defence of the colony (Burger and Hahn, 1977; Jullien and Clobert, 2000; Arroyo et al. 2001), but different studies have also highlighted the role of inter-specific attraction in territorial species (Slagsvold 1980; Mönkkonen et al. 1990; Forsman et al. 2002).

Farmland passerine birds can be thought of as an ecological guild of small-sized, ground nesting and open habitat specialists (Suárez et at. 1997) that largely coincide in their habitat preferences at the landscape scale (Tellería et al. 1988; Delgado and Moreira 2000),

and rely on low-intensity agricultural habitats for their survival and reproduction (Suárez et al. 1997). Several studies have focused on how closely related and sympatric steppe birds partition habitat resources, thereby favouring their coexistence at the landscape scale (Suárez et al. 2002; Serrano and Astrain 2005; Morales and Traba 2009), although very few have evaluated the role of inter-specific attraction or association in their habitat selection patterns (see Martín et al. 2010).

In this paper, we study the pattern of inter-specific association of breeding territories in a passerine assemblage of dry cereal farmland and evaluate the role of the presence of heterospecifics in the habitat use patterns exhibited by different species, discussing the relative role of overlapping habitat use patterns and the potential attraction effect exerted by some species. Among the habitat factors, agricultural management variables were considered, so that the management implications of our results for the species and community assemblage can be discussed.

Methods

Study area

The study was conducted in a 900 km2 flat dry cereal farmland area in the Madrid region, central Spain (Fig. 1). Traditional land use has produced a dynamic agricultural mosaic in the area, with fields of different size (range 0.5-30 ha) and varying development of field boundaries. The typical rotation on a given field has a two-year cycle, with alternating cereals and annual fallow. Therefore, winter wheat and barley and annual fallows (hereafter, arable land) are dominant,

covering ca. 80% of total area. The rest is long-term fallow (more than two years old), pastures and, marginally, woody crops (some vineyards and olive orchards). Cereal yield in the study area is around 3000 kg ha^{-1}, which is high in the Spanish context, but still low in the European one (Bignal & McCracken, 1996).

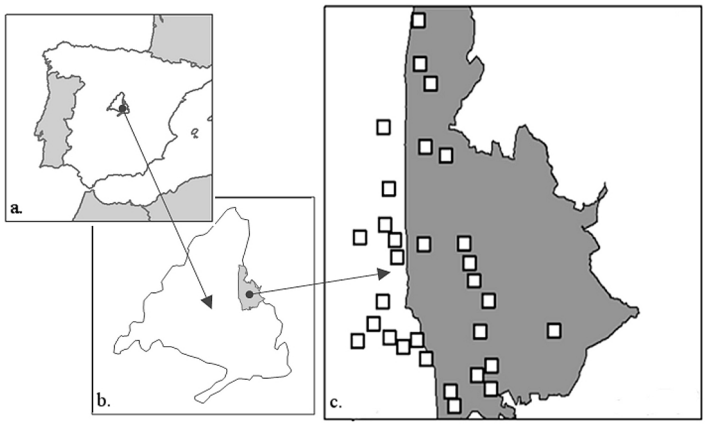


Fig. 1. Location of the study area (a) in the region of Madrid (b), and of survey plots within the study area (c).

The farmland passerine assemblage.

The species considered were the corn bunting (*Emberiza calandra*), the crested lark (*Galerida cristata*), the fan-tailed warbler (*Cisticola juncidis*), the tawny pipit (*Anthus campestris*) and the short-toed lark (*Calandrella brachydactyla*). This group constitutes a guild of open habitat and ground nesting specialists, typical of Mediterranean cereal pseudo-steppes (Suárez et al. 1997; Traba et al. 2007; Massa and La Mantia, 2010). These species share general habitat preferences at the landscape scale, selecting open farmland areas dominated by a mosaic

of cereal crops, fallows and pastures, and including some patches of natural vegetation (Tellería et al. 1988; Delgado and Moreira 2000).

Bird surveys

Field work was conducted in spring 2007. Birds were surveyed three times during the local breeding period (April 15th – June 15th), approximately every three weeks, in 30 500 x 500 m plots centred in a focal cereal field. Depending on the size of these focal fields, each survey plot might comprise more fields with cereal crops and/or fallow land. To avoid pseudo-replication and minimise the effect of spatial autocorrelation, survey plots were at least one kilometre apart. Surveys took place between one hour after dawn and until noon, but only if it was not windy, cloudy, or raining, and were conducted by slowly walking the entire census area, so that each spot was no further than 100 m from the surveyor's route. This is a modified version of the British Trust for Ornithology Common Bird Census protocol (Bibby et al. 1992).

Breeding bird territories were determined for the study species using the three survey rounds. Two different criteria were used to define breeding bird territories, depending on the species' detectability and breeding behaviour. To meet the criteria for assigning a breeding territory, species of category A (corn bunting, crested lark, short-toed lark, and fan-tailed warbler) had to be observed at least twice displaying territorial behaviour (calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds. Category B comprised species unlikely to be present during all the three survey visits because of their migration behaviour (i.e., long-distance migrants arriving relatively late: tawny pipit). For this

category, only one observation of territorial behaviour was required. This conservative method avoids overestimation of territory abundance.

Table 1. Description and summary statistics of landscape and field management variables used to analyse the relationships between bird breeding territories and habitat.

Variable	Description	Mean ± SD
Share of arable land	Percentage of surface covered by arable land in survey plots	80.01± 13.35
Share of non-cultivated area	Percentage of surface covered by non cultivated patches in survey plots	13.78± 11.00
Field size	Focal field size (ha)	5.48 ± 5.34
Herbicide	Number of herbicide applications in focal field	0.63 ± 0.61
Yield	Cereal grain (ton/ha) obtained in focal field	3.14 ± 1.24

Environmental variables

Information about agricultural management was gathered through a questionnaire sent out to collaborating farmers owning the cereal focal fields in which the bird survey plots were centred, as well as up to five more cereal fields (depending on availability) within each of 30 squares 1x1 km, each containing one bird survey plot. Therefore, data about farming practices were based either on a single large cereal field (which could, in fact, occupy most of the plot) per survey plot, or on the average of up to five smaller cereal fields within each survey plot belonging to the same farmer (Table 1).

Three characterizing landscape variables were estimated within 500-m- radius circles centred on each survey plot: mean field size, share of arable land and share of non-cultivated land (see Table 1). These variables have been shown to determine the distribution and abundance of farmland birds in several studies (e.g. Brotons et al.

2005; Wolff 2005) These measurements were done using digitized maps from ortho-images of the study area and Patch Analyst 3.12 extension to ArcView (see Rempel et al. 1999).

Data analyses

In order to identify and statistically test the pattern of inter-specific association of the entire assemblage in the study area, presence/absence data for breeding territories of the different species in each survey plot were analysed with the Ecosim program for co-occurrence analysis (Gotelli and Entsminger 2009). This software applies Montecarlo simulation procedures to generate random distributions of species' presence and absence in a series of sites (e.g. islands in an archipelago) and produce a null distribution model to test hypotheses on species segregation or association (Gotelli 2000). The survey plots used in this study were considered suitable for evaluating potential inter-specific clustering because they were isotropic, predominantly flat (thus offering birds large visibility ranges and the opportunity to interact) and relatively landscape-homogeneous (dominated by grassy vegetation and lacking sources of landscape heterogeneity such as trees or buildings). Therefore, considering each survey plot as a different site, the recommendations of Gotelli (2000) and Gotelli and Entsminger (2009) were followed for simulation constraints. Empty sites were included, assuming the predicted occurrence of the different species to be proportional to their observed occurrence (row sums proportional). The probabilities of occupation were assumed to be equal for all sites (column sums equiprobable). These constraints produce a negligible bias and make the smallest number of assumptions (Gotelli and Entsminger 2009). The simulation

procedure used 5000 iterations. As a co-occurrence index, the C-score (Stone and Roberts 1990) was selected to evaluate the inter-specific association pattern. This index measures the average number of co-occurrences among all unique pairs of species in the assemblage, and minimises Type I error probabilities (Gotelli and Entsminger 2009).

Subsequent analyses relating abundance patterns and habitat selection were restricted to the corn bunting, the fan-tailed warbler and the crested lark, due to the small number of presence data and low territory abundance in the cases of the short-toed lark and the tawny pipit. Prior to these analyses, however, we tested for potential spatial autocorrelation in the territory abundance data of those three species by means Moran's Index correlograms, using the PASSAGE software (Rosenberg 2009). Due to the lack of normality of territory abundance data, the Mann-Whitney test of differences between two independent samples was applied to evaluate patterns of abundance variation in breeding territories of each of the three species considered in relation to the other two.

Habitat preferences of these three species were evaluated by means of classification tree analyses (De'Ath and Fabricius 2000). This classification-regression technique allows the identification of thresholds in individual habitat variables that maximise the probability to find a species. The use of a presence-absence analysis, such as classification trees, is justified given the obtained distribution of territory abundance data, which showed little variation and approached a 0-inflated Poisson function. On the other hand, classification trees maximize sample size as compared to other

presence-absence methods, such as binomial regression, in which the sample is limited by the number of presences. Classification trees deal adequately with non-linear relationships between response and predictor variables, and interactions between predictors (De'Ath and Fabricius 2000; Carrascal et al. 2006). Additionally, this method provides a hierarchical procedure for the selection of relevant variables (Carrascal et al. 2006; Kristian 2006).

Given the explanatory purpose of these analyses (De'Ath and Fabricius 2000) and the sample size limitations (N = 30 survey plots), no sub-sample for model cross-validation was reserved. In a first step, classification trees were used to identify relevant habitat variables for each species without including as categorical predictors the presence/absence of the other two species in the same survey plots. Therefore, this step provided and idea of each species' habitat preferences at the landscape scale considered. In a second step, the trees were re-built for each species including as categorical factors the presence/absence of the other two. The results were then compared to assess the influence of the other two species on each species' habitat preferences. A model deviance-based procedure was used to prune the trees (De'Ath 2000; Statsoft 2008) with a minimum sample size of 5 as criterion to stop tree building. This procedure minimizes tree over-parametrization. Abundance and classification trees analyses were performed in Statistica 8.0 (Statsoft, 2008). Additionally, Statistica provides a ranking of variables according to their importance in the tree, which is the summed relative contribution of each variable to the variability explained at each node of the tree, prior to pruning (Breiman et al. 1984; Statsoft 2008).

Results

Inter-specific association pattern

Corn bunting territories were present in 15 out of the 30 survey plots, whereas crested lark territories were present in 12 of them, and fan-tail warblers ones were present in 14 of them. The distribution of observed presence/absence data of the five species in the assemblage was significantly different from the null model distribution generated by Ecosim (Fig. 2). This yielded a mean value for simulated C-scores significantly higher than that calculated with the observed presence/absence data (observed C-score = 8.70, simulated C-score = 29.5, p = 0.0002). This result indicates a pattern of non-random association, that is, spatial aggregation, over the 30 survey plots among the passerine species considered.

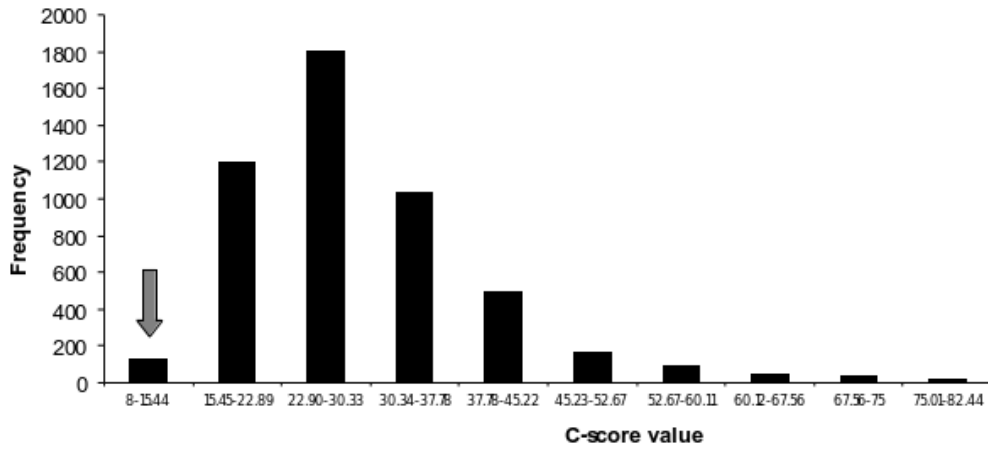


Fig. 2. Histogram showing the frequency distribution of C-score values obtained by means of Ecosim Montecarlo simulation. The C-score quantifies the average amount of co-occurrence between all possible pairs of species in the assemblage. The grey arrow indicates the histogram class containing the observed C-score value.

Abundance patterns

No significant spatial autocorrelation was found in territory abundance data for any of the three species considered (Moran's I correlogram p> 0.1 in all cases). Crested lark breeding territories (CLT hereafter) were significantly more abundant in survey plots where corn bunting territories (CBT hereafter) were present than in those where these were absent (Mann-Whitney U test, adjusted Z = 2.79, p = 0.005, $N_{present}$ = 15, N_{absent} = 15) and vice versa (Mann-Whitney U test, adjusted Z = 2.73, p = 0.006, $N_{present}$ = 12, N_{absent} = 18). Similarly, fan-tailed warbler territories (FWT) were significantly more abundant where co-occurring with CBT (Mann-Whitney U test, adjusted Z = 3.60, p = 0.0003, $N_{present}$ = 15, N_{absent} = 15) and vice versa (Mann-Whitney U test, adjusted Z = 3.30, p = 0.001, $N_{present}$ = 14, N_{absent} = 16). However, abundance of CLT or FWT did not differed significantly between plots with and without breeding warblers (Mann-Whitney U test, adjusted Z = 1.65, p = 0.10, $N_{present}$ = 14, N_{absent} = 16) or crested larks (Mann-Whitney U test, adjusted Z = 1.82, p = 0.07, $N_{present}$ = 12, N_{absent} = 18), respectively, although in both cases territories tended to be more abundant in presence plots.

Habitat use patterns

Up to 87% of all samples for corn bunting were correctly classified (100% of presences and 73% of absences), with mean field size and the share of arable land as the main variables influencing the distribution of the species (Fig. 3a). Field size was the first criterion for sample splitting and showed a negative effect, with 66% of

presences occurring in plots where mean field size was smaller than 3.57 ha. For the remaining 34%, the next classification criterion was the share of arable land, with 80% of these presences (in fact 4 out of 5, which is 27% of the total presences) occurring in plots with share of arable land lower than 65.63%. Again, field size was used to classify the remaining sample, so that the only presence included (6.7 % of total presences) corresponded to mean field size smaller than 1.04 ha. The relative importance of all variables is presented in Fig. 3b.

The corresponding tree including presence of CLT and FWT as categorical predictors correctly classified 100% of presences and 80% of absences. Presence of the FWT was the first criterion for classification, so that 87% of predicted corn bunting presences occurred in plots with warbler presence. Presence of CLT predicted the occurrence of the only two presences of corn bunting that remained unclassified (Figs. 3c, d).

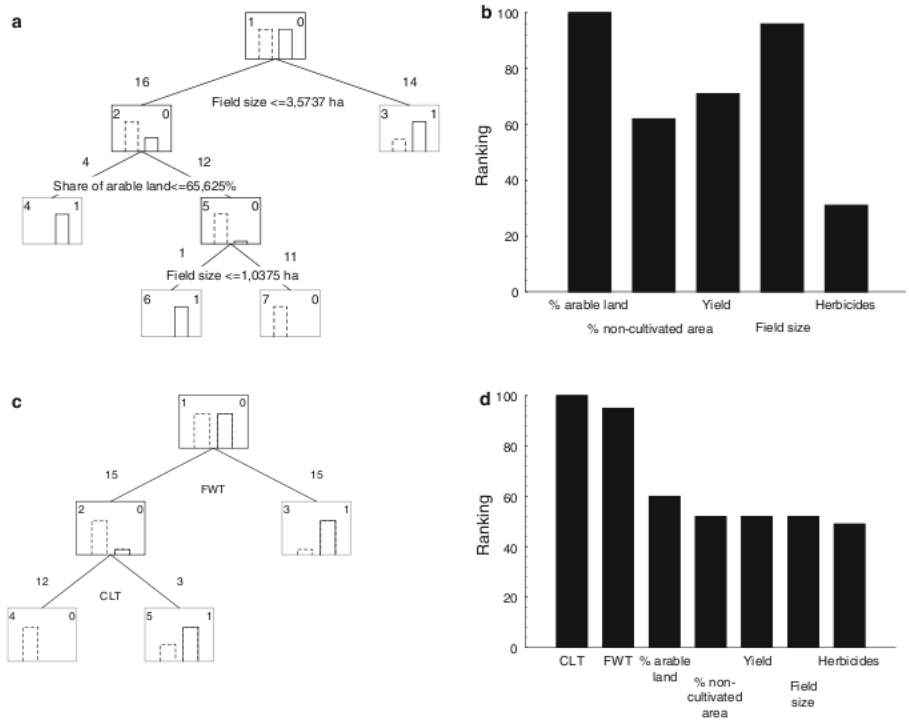
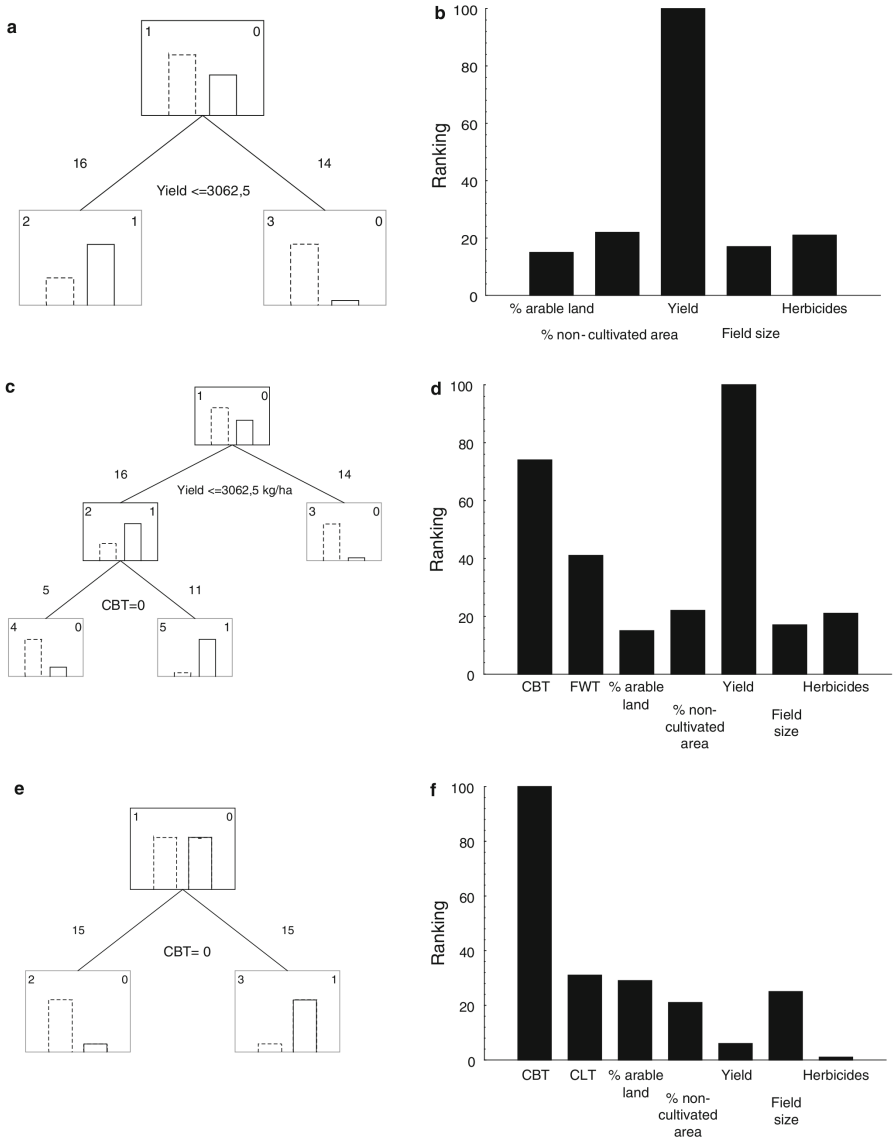


Fig. 3. Results of the classification tree analysis of presence/absence of corn bunting breeding territories in the study area: (a) classification tree of territory occurrence irrespective of the presence or absence of other breeding species; (b) relative importance of the environmental variables considered in such analysis (see Methods for explanation); (c) classification tree of territory occurrence considering territory presence or absence of crested lark (CLT) and fan-tailed warbler (FWT); (d) relative importance of the environmental variables considered in such analysis. In the classification trees, black boxes indicate split nodes and grey boxes indicate terminal nodes. Numbers in the boxes' upper-left corners correspond to node numbers, and numbers in the upper-right corner denote the predicted class (absences [0] or presences [1]) to which the corresponding node belongs. Numbers above tree branches show the number of cases falling in each child nodes and labels between splitting branches indicate the environmental variable used as splitting criterion and by its corresponding threshold value. The histogram inside nodes shows the number of cases corresponding to presence (solid line) and absence (stripped line) of corn bunting territories.


a
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0
16
14
Yield <=3062,5
2
1
3
0
b
Ranking
100
80
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40
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Yield
Herbicides
% non- cultivated area
Field size
c
1
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16
14
Yield <=3062,5 kg/ha
2
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3
0
5
11
CBT=0
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Ranking
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Yield
Herbicides
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CBT= 0
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100
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CBT
CLT
% arable land
Yield
Herbicides
% non-cultivated area
Field size

◀

Fig. 4. Results of the classification tree analysis of presence/absence of crested lark and fan-tailed warbler breeding territories in the study area: (a), classification tree of crested lark territory occurrence irrespective of the presence or absence of other breeding species; (b) relative importance of the environmental variables considered in such analysis (see Methods for explanation); (c) classification tree of crested lark territory occurrence considering territory presence or absence of corn bunting (CBT) and fan-tailed warbler (FWT); (d) relative importance of the environmental variables considered in such analysis; (e) classification tree of fan-tailed territory occurrence considering territory presence or absence of corn bunting (CBT) and crested lark (CLT); (f) relative importance of the environmental variables considered in such analysis. In the classification trees, black boxes indicate split nodes and grey boxes indicate terminal nodes. Numbers in the boxes' upper-left corners correspond to node numbers, and numbers in the upper-right corner denote the predicted class (absences [0] and presences [1]) to which the corresponding node belongs. Numbers above tree branches show the number of cases falling in each child nodes and labels between splitting branches indicate the environmental variable used as splitting criterion and by its corresponding threshold value. The histogram inside nodes shows the number of cases corresponding to presence (solid line) and absence (stripped line) of corn bunting territories.

Discussion

Inter-specific association pattern

Breeding territories of the analyzed species tended to occur together or to be absent in the same survey plots. This means that reproduction of these species is linked to the same areas within the landscape and that inter-specific competition is probably not the main process involved in assemblage formation (Gotelli and McCabe 2008). Although some simulation studies have shown that non-random patterns of species co-occurrence could also arise from ecological drift (Ulrich 2004), the detected association pattern and habitat relationships suggest that the assemblage might result, at least in part,

from positive inter-specific interaction. Regarding the three most abundant species, our results suggest that the corn bunting might be playing a key role in the assemblage, given that crested larks and fan-tailed warblers tended to be more abundant wherever the corn bunting was present, while the lark was not necessarily more abundant in plots where the warbler was present and vice-versa. This possibility is strengthened by results from other studies in extensive farmland (Brambilla et al. 2009), where similar positive associations between the corn bunting and other bunting species were found.

Habitat use

The habitat use pattern of the fan-tailed warbler did not depend on any of the landscape scale habitat variables considered, whereas for the crested lark, yield was the only significant variable. Yield is a reliable indicator of intensification (Tilman et al. 2002), a large scale process with negative effects on several taxa (Geiger et al. 2010). Consequently, these two species can be considered relatively habitat-generalist at landscape scale and, in the case of the fan-tailed warbler, relatively more tolerant to yield increases. Contrarily, a marked habitat use pattern was found for the corn bunting. When introduced in the classification tree, the presence/absence of corn bunting was the most important variable explaining the occurrence of warbler territories, and the second most important one explaining that of lark territories, which suggests that corn bunting habitat preferences would be influencing the distribution of the other two species and would point out to corn bunting habitat preferences as a potentially influential factor in assemblage formation.

When the presence of heterospecifics was not considered, the share of arable land and field size appeared as the most important variables limiting the distribution of corn buntings, which is consistent with existing knowledge about habitat selection of this species (Eislöffel 1997; Brickle et al. 2000; Brambilla et al., 2009). Territorial corn buntings use to sing and survey from perching elements (tall grasses, isolated bushes, fences), particularly available along field boundaries and on fallow land, which are a main source of insect and seed food for adults and nestlings (Brickel et al. 2000). Since the abundance of these landscape elements tends to be inversely proportional to field size (e.g. Baessler and Klotz 2006), the negative effect of this variable is readily understandable. Availability of uncultivated patches in the landscape is also negatively associated to the dominance of arable land and resulting landscape homogenisation (Benton et al. 2003). The identified detrimental effect of the share of arable land on corn buntings could then be regarded as another result of agricultural intensification. The threshold value is 65.5% of arable land in the study area, which means that corn bunting tolerates certain crop dominance in the landscape, but avoids fully cultivated areas (see also Brambilla et al. 2009).

Therefore, our results identify the corn bunting as a species sensitive to agricultural intensification, in congruence to what has been described in other European study areas (Brickle et al. 2000; Perkins et al. 20011; Brambilla et al. 2009). This conclusion is strengthened by the relatively high importance attributed by the analysis to cereal yield, a good indicator of intensification (Tilman et al., 2002; Geiger et al., 2010).

Nevertheless, when presences of heterospecifics were included in the classification tree, these variables showed high explanatory power. Corn buntings were found mainly where fan-tailed warblers and crested larks were present, although landscape structure (e.g. share of arable land) and agricultural management (field size, yield) globally maintained their relatively higher importance. This result is also consistent with the inter-specific aggregation pattern detected by the co-occurrence analysis.

In relation to the crested lark and the fan-tailed warbler, their weaker habitat use patterns at the scale considered (landscape) can be interpreted as a result of their more generalist habitat preferences at such scale (which, of course, does no preclude the existence of stronger habitat preferences at smaller or microhabitat scales). As to the fan-tailed warbler, this result is consistent with the few available studies on the species in farmland areas, which showed no particularly strict habitat preferences at the landscape scale as long as cereal cultivation, and particularly wheat, was dominant (Delgado and Moreira 2000; Moreira et al. 2007). Neither research in wetland areas detected strict habitat use patterns for this species when compared to other assemblage members (Martínez-Vilalta et al. 2002). Regarding the crested lark, previous studies have identified this species as a habitat generalist, both in farmland (Moreira et al. 2007; Suárez et al. 2009) and semi-deserts (Guillaumet et al. 2010). This is consistent with our results since, apart from yield, no other habitat variable was included in the classification tree for this species. Moreover, the detected threshold yield value can be considered high in the context of Iberian agricultural areas, suggesting that the crested lark tolerates moderate levels of agricultural intensification.

Inter-specific interactions

Our results suggest a relevant role of inter-specific interactions in these species' patterns of habitat use, although they do not necessarily exclude the role of coinciding broad habitat preferences. It can be reasonably concluded from the above discussion that corn buntings avoid the most intensified and high yielding areas in the landscape. Fan-tailed warbler and crested lark territories tend to occur in their vicinity (although nesting larks also avoid the highest yielding areas), thus probably benefiting from the proximity of field boundaries and uncultivated patches that provide the required insect food. In fact, corn bunting territory presence could be functioning as a breeding habitat-quality surrogate for the other two species (and, potentially, other farmland birds) as it has been shown in other studies, both at the intra-specific (Betts et al. 2008), and at the hetero-specific levels (Hramada et al 2009). In fact, corn buntings establish their territories early in the season (as early as February in some parts of the Mediterranean Region, Snow and Perrins 1998), and thus they should be present and 'available' as potential habitat surrogates by the time the others settle (for example, *Galerida* larks and the fan-tailed warbler rarely settle before April, see Snow and Perrins 1998 and Suárez et al. 2009).

Another interesting and also non-exclusive possibility is that fan-tail warblers and crested larks would be benefiting from the anti-predator vigilance provided by perching corn buntings, increasing their survival and rates of breeding success. These predation-mediated positive interactions have been observed in other species and

ecological contexts, both in wintering (Martín et al. 2010) and territorial breeding birds (Slagsvold 1980; Forsman et al. 2002).

Conservation implications

The potential association between these three (and potentially more) species may have relevant conservation implications. If increasing intensification eliminates corn bunting territories from a given farmland area, the associated species could also tend to disappear. In this context, our results are consistent with previous studies on farmland passerines (e.g. Brickle et al. 2000; Delgado and Moreira 2000; Brambilla et al. 2008, 2009): in order to maintain these species' populations, farmland management should guarantee the mosaic landscape configuration that combines extensive cereal crops (thus minimizing the negative effects of high-yielding oriented management, to which species like the corn bunting and the crested lark are sensitive) and fallow land, avoiding too large field size and keeping uncultivated field borders as a source of food and shelter. Therefore, the corn bunting might function as a 'key' species in the farmland bird assemblage, and its spatial distribution might probably play a relevant role in the meta-community dynamics, which would also be coherent with results of Brambilla et al. (2009). In any case, and given the marked species co-occurrence pattern revealed by the Ecosim analysis, the disappearance of the assemblage due to agricultural intensification (or any other source of disturbance) could considerably limit re-colonization by a more or less complete community.

Acknowledgements

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CAPÍTULO V

La intensificación agraria a escala local modula la redundancia funcional en las comunidades de plantas arvenses mediterráneas.

Este capítulo reproduce íntegro el siguiente manuscrito:

Guerrero, I.; Carmona, C. P.; Morales, M. B.; Oñate, J. J. y Peco, B. (2013) Field-level intensification modulates functional redundancy in Mediterranean arable plant communities. Manuscrito en revisión en PloS ONE

Resumen

Las plantas arvenses juegan un papel vital en los agro-ecosistemas, pero su diversidad taxonómica está severamente afectada por la intensificación agraria. Sin embargo, no está claro si el descenso en diversidad de especies viene acompañado de un cambio de diversidad funcional equivalente, lo cual afectaría a la provisión de servicios en el agro-ecosistema. Analizamos la respuesta de cuatro rasgos funcionales (área foliar específica, altura, peso de semilla e inicio de floración) a la intensificación agraria de una comunidad de plantas arvenses en un sistema cerealísta mediterráneo. Mediante análisis de regresión, exploramos las relaciones entre las medias ponderadas (CWM) y la diversidad funcional (FD) de cada rasgo con la intensificación agraria a escala local y de paisaje. Exploramos también los cambios en la relación entre la riqueza específica y la diversidad funcional para cada rasgo y los cambios en esa relación a lo largo de los gradientes de intensificación agraria.

La intensificación a nivel local mostró un importante efecto en CWM y FD de los rasgos estuidados, mientras que la intensificación a escala de paisaje no mostró ningún efecto sobre estas características. La intensificación a nivel local favoreció especies altas, con mayor peso de semillas, mayor área foliar y con floración más temprana. La FD de la altura decreció con mayores niveles de intensificación, mientras que las FD de peso de semilla e inicio de floración aumentaron sugiriendo la invasión de la comunidad por especies adaptadas a mayores niveles de productividad asociados a la intensificación. Encontramos, además, evidencia de efectos no lineales de la gestión agrícola a nivel de campo de cultivo sobre la redundancia funcional en las comunidades de plantas arvenses. Se produjo una importante pérdida de especies con rasgos redundantes durante los primeros estadios de intensificación. El consiguiente aumento de la intensidad de uso del suelo resultó en cambios en la FD de las comunidades sin cambios en la riqueza específica.

Nuestros resultado aportan nuevas consideraciones acerca del impacto de la gestión agrícola sobre la estructura de las comunidades de plantas arvenses, a través de sus efectos no lineales sobre la redundancia funcional. Este tipo de respuestas deberían tenerse en cuenta en el diseño y adopción de estrategias de gestión orientadas a la conservación de la biodiversidad en los agro-ecosistemas.

Abstract

Arable plants play key roles in agro-ecosystems, but their species diversity is severely affected by agricultural intensification. However, it remains unclear if declining species diversity is accompanied by similar changes in functional diversity, which would ultimately affect the provisioning of agro-ecosystem services. We analyzed the response of four functional traits (specific leaf area, canopy height, seed mass, flowering onset) to intensification of agricultural management in a Mediterranean cereal crop arable plant community. We performed regression analyses to explore the relationships between Community Weighted Mean (CWM) and Functional Diversity (FD) for each trait and agricultural intensification at field and landscape levels. We also explored the changes in the relationship between species richness and the functional diversity of each trait and the changes in this relationship along the intensification gradients.

Field-level intensification had a remarkable effect on the CWM and FD of the studied traits, while intensification at the landscape level did not have any effect on these features. Field-level intensification favored tall and heavy-seeded species, with high specific leaf area and early flowering. The FD of plant height decreased with field-level intensification, while the FD of seed mass and flowering onset increased, suggesting an invasion of the community by species adapted to higher levels of productivity associated with intensification. We found evidence for non-linear effects of field-level management intensification on the functional redundancy in arable plant communities. An important loss of species with redundant traits occurred along the first stages of intensification. Further levels of intensification resulted in changes in the FD of communities without changes in species richness.

Our results provide new insights on how agricultural management impacts arable plant community structure, through its non-linear effects on functional redundancy. This type of responses should be taken into consideration when designing and adopting management strategies targeting biodiversity conservation in agricultural systems.

Introduction

Species richness and its supporting role in connection to ecosystem functions and services have received great attention in the literature studying the impacts of agricultural intensification on biodiversity (see review by Kleijn *et al.* 2011). The global and complex process of agricultural intensification involves management changes at individual field level (such as the use of high-yielding crop varieties, chemical fertilizers and pesticides, irrigation, mechanization and, sometimes, abandonment), aimed to increase yields. These actions result also in an aggregated outcome at the landscape scale (simplification, homogenization, artificialisation). As a consequence, complex and detrimental effects on biodiversity and agro-ecosystem properties are usually associated to intensification (e.g. Kremen, Williams & Thorp 2002; Donald *et al.* 2006; Stoate *et al.* 2009; Geiger *et al.* 2010; Guerrero *et al.* 2012).

In the last decades, farmland biodiversity has been the focus of important conservation efforts in Europe, including various common policy tools, such as the Nitrates, Birds and Habitats Directives and agri-environment schemes (Beaufoy 1998; Buller, Wilson & Höll 2000; Primdahl *et al.* 2003). Despite these efforts the negative effects of agricultural intensification on European farmland biodiversity persist (EEA 2010).

However, it remains unclear whether changes in species diversity are accompanied by similar changes in the provisioning of ecosystem services in agro-ecosystems (e.g. Letourneau & Bothwell 2008; Macfadyen *et al.* 2009). Recently, researchers' attention has shifted to

functional diversity (FD; i.e. the value and range of functional traits of the organisms in a community) as a reliable proxy of the range of functions provided by a community (Díaz & Cabido 2001; Hooper *et al.* 2005). It is generally assumed that the loss of species associated to land use intensification results in a similar loss of functional diversity. However, this assumption has been recently challenged (Mayfield *et al.* 2010), since the changes in species richness and functional diversity after intensification, although often positively correlated, could follow different trajectories, depending on the degree of functional redundancy in the community (i.e. the number of species possessing similar functional traits, see Rosenfeld 2002) and on how changes in land management affect community assembly processes. In fact, species richness may decline without a corresponding loss of functional diversity in communities with high functional redundancy (Flynn *et al.* 2009) and it may even be possible for functional diversity to increase without a change in species richness, thanks to changes in environmental filters favoring the invasion of functionally different species (Mayfield *et al.* 2010). These models have recently been tested along intensification gradients in grassland ecosystems (Carmona *et al.* 2012; Peco *et al.* 2012) but not in arable systems.

In this paper we explore the relationship between species richness and functional diversity along intensification gradients focusing on wild plants growing on agricultural fields (from now on, arable plants, *sensu* Storkey 2006). Arable plants are well adapted to disturbed and resource–rich environments such as agricultural fields, thanks to a functional trait composition that makes them good colonizers, reproducers and/or survivors (Sutherland 2004). Due to their position at the base of trophic webs, arable plants are essential to other taxa

(Scherber *et al.* 2010; Evans *et al.* 2011; Brooks *et al.* 2012; Ebeling *et al.* 2012), including species providing important ecosystem services, such as biological pest control and pollination (Kremen, Williams & Thorp 2002; Thies *et al.* 2011; Winqvist, Ahnstrom & Bengtsson 2012). They contribute as well to maintain an adequate vegetation structure within cropped fields, determining the quality of agricultural habitats for invertebrates, birds and mammals (Benton, Vickery & Wilson 2003; Marshall *et al.* 2003). Nevertheless, these species are worryingly affected by the intensification of agricultural practices focused on combating the potentially negative impact that they have on crop yield (Guerrero *et al.* 2010; Storkey *et al.* 2012). But diversity of arable plants at the field level also depends on the configuration of the surrounding landscape, with local diversity increasing with landscape complexity (Gabriel, Thies & Tscharntke 2005).

We analyzed the response of four arable plant functional traits (specific leaf area, canopy height, seed mass and flowering onset) to agricultural intensification gradients, separating field and landscape levels, to discern how the relationship between arable plant species richness and the functional diversity of each trait changes along these intensification gradients. Specifically, we expected that: (i) increased productivity related to agricultural intensification induces changes in functional trait composition of arable plant communities towards trait values associated to faster resource-use strategies; (ii) intensification of agricultural practices reduces functional diversity, eliminating functional types poorly adapted to high nutrient levels; and (iii) functional redundancy in these communities is high because of the strong filtering of trait values for wild plants growing among crops,

but decreases with field management intensification. We found supporting evidence of non-linear effects of field-level management intensification on functional redundancy, which provides new insights on the interactions between agricultural management and arable plant community structure.

Materials and methods

Study area

The study was conducted in a ca. 500 km^2 dry cereal farmland area in central Spain (40° 40' N, 3° 25' W; altitudes ranging from 600 to 800 m.a.s.l.). Average annual temperature is 14.1° C with hot summers and mild winters and average annual rainfall is ca. 400 mm, concentrated in spring and autumn (AEMET 2008). These climatic, terrain and soil characteristics define a rather homogeneous area for rainfed cereal cropping (Appendix 2). Traditional land use has produced a dynamic agricultural mosaic in the area, with fields of different size (in the range of 0.5–30 ha) and varying development of field boundaries. Non-irrigated winter wheat and barley and annual fallow (fields left un-sown in a given year) are dominant, covering ca. 86% of total area. The rest is long-term fallow (more than two years old), shrubs and, marginally (0.60% of total area), olive groves and vineyards. Typical rotation on a given field has a two-year cycle, with alternating cereals and fallow. Cereal yield in the study area is around 3000 kg ha^{-1}, lying within the range of central Spanish drylands (average ± SD is 3256 ± 710 kg ha^{-1}; MARM 2008), but still low enough to consider this system as low-intensity in the European context (Bignal & McCracken 1996).

Field data collection

A total of 78 agricultural fields sown with winter wheat were sampled in spring 2007, an average year regarding temperatures and rainfall in the area (AEMET 2008). One to five sampling points were distributed in each field depending on field size, in order to homogenize sampling effort. To avoid field margin effects on observations, sampling points were placed at 10 m from the margin. Arable plant species were surveyed between May 27th and June 25th. Three 2×2 m^2 vegetation quadrats per sampling point were located. Quadrats were placed parallel to the field side and 5 m apart from each other. The percentage of cover of each species within the quadrat was estimated and averaged for each sampling point and subsequently averaged per field when more than one sampling point per field were present. Finally, species richness was calculated as the number of species found on each sampling point.

Agricultural intensification data

Three variables related to field management practices and three related to landscape structure were considered (Table 1). Information about Yield, a frequently used proxy of agricultural intensification (e.g. Green *et al*., 2005), and farming practices (Applied Nitrogen Fertilizer and Sowing Density) during the sampling year was collected by means of a questionnaire sent out to farmers managing each field. Information on landscape structure variables was obtained from digital maps and measured within circles with a radius of 500 m around the centre of each sampling point. Data on each variable were averaged where more than one sampling point per field were present (Guerrero *et al*. 2010).

Table 1. Description and summary statistics of field management and landscape level variables used to characterize sampled cereal fields (*n* = 78) and Principal Component Analysis loadings in factors summarizing field-level (PC1) and landscape level (PC2) management characteristics of sampled fields. All variables adjust to a normal distribution (Kolmogorof-Smirnov test, $P < 0.05$) except Sowd and Mfs_500, which were ln(x+1) transformed.

Variable	Description	Mean ± SD	PC1	PC2
Field management				
Fertilizer (Fert)	Total kg/ha nitrogen applied on focal field	59.47 ± 33.46	0.797	0.125
Sowing density (Sowd)	Density (kg/ha) of seed sown	204.17 ±70.23	0.682	0.010
Yield (Yield)	Cereal grain (ton/ha) obtained in focal field	3.02 ± 1.22	0.832	-0.127
Landscape characteristics				
Field size (Ffs)	Focal field size (ha)	4.47 ± 5.24	0.127	0.870
Mean field size (Mfs_500)	Mean size (ha) of fields with arable crops within a circle radius 500 m centered in the sampling point	3.54 ± 4.21	0.050	0.857
Arable land cover (Arable_500)	Percentage of cultivated land within a circle radius 500 m centered in the sampling point	62.08 ±26.27	-0.383	0.519
Proportion of variance explained			0.326	0.299
Cumulative variance explained			0.326	0.625

Functional traits

Following Westoby (1998), three representative traits of plant strategy for resource capture and allocation were selected: Specific Leaf Area (SLA, $mm^2\ mg^{-1}$), mean canopy height (cm) and seed mass (mg). Flowering onset (month, ranging from January to September) was further included, a trait that has been frequently used in studies analyzing the response of vegetation to agricultural intensification (e.g. Storkey, Moss & Cussans 2010; Peco *et al.* 2012). Functional trait data were extracted from LEDA and e-FLORA-sys databases (Kleyer *et al.* 2008) for 105 sampled species (see (see Table S1, Supporting Information). Species with trait information represented an average percentage cover of ca. 95%.

Prior to any calculation, trait values were log-transformed and then standardized to a 0-1 scale. For each functional trait and field, Community Weighted Mean (CWM) and Functional Diversity (FD) were calculated. CWM can reveal changes in optimal trait values along the studied intensification gradients (Ricotta & Moretti 2011; Mason *et al.* 2012) and was calculated averaging for each trait the values of all the species present in the field, weighted by their covers. FD, which can be used as an indicator of the effects of agricultural intensification on the patterns of convergence or divergence in trait values (Mason *et al.* 2012), was calculated as the weighted standard deviation of each trait values of all species present in the field. Using the same index of functional diversity that has previously been used in works studying the changes in functional diversity associated with land use changes (Mayfield *et al.* 2010; Peco *et al.* 2012) allows the comparability of results.

Statistical analyses

Principal Component Analysis (PCA) was applied to the data matrix with 6 variables on agricultural intensification and 78 agricultural fields. Two orthogonal axes were obtained: one was contributed by Yield, Sowing Density and Applied Nitrogen Fertilizer and was thus related to field management practices (PC1); the other was contributed by Proportion of Arable Land, Mean Arable Field Size and Sampled Field Size and was related to landscape structure (PC2). Both axes explained together 63% of total variance (Table 1).

Two sets of regression analyses were performed with CWM and FD of the four selected traits as response variables respectively and using in both cases intensification at field level (scores on PC1) and at landscape level (scores on PC2) as explanatory variables.

We explored how agricultural intensification at field level modulates the relationship between species richness and FD. Changes in these parameters for each trait (ΔDSF vectors, Mayfield *et al.* 2010) along the intensification gradient were graphically explored by ascribing the fields to one of the four categories corresponding to the four equal-length intervals of increasing intensification along PC1. Variation between these intervals in species richness and FD of each trait were analyzed by means of MANOVA and differences between intervals were analyzed with Tukey's HSD post-hoc test.. All the analyses were performed using the program R version 2.13.1 (R Development Core Team 2011).

Results

CWM of all the studied traits were significantly correlated with intensification at field level (PC1), which favored tall, heavy-seeded species, with high SLA values and early flowering (Fig. 1). Significant correlations were also found between PC1 and FD of three of the studied traits, with intensification increasing FD of seed mass and flowering onset and reducing FD of plant height (Fig. 2). In contrast, the axis describing the intensification gradient at landscape level (PC2) was not a significant predictor of either CWM or FD of the studied traits (Table 2).

Table 2. Results of regression analyses evaluating the effect of agricultural intensification at landscape level (PC2) on Community Weighted Mean (MWC) and Functional Diversity (FD) values of the four traits sampled in fields.

	$F_{1,76}$	Adjusted R^2	P
CWM Height	1.42	0.01	0.24
CWM Specific leaf area	1.23	0.00	0.27
CWM Seed mass	2.13	0.01	0.15
CWM Flowering onset	0.01	-0.01	0.94
FD Height	1.71	0.01	0.19
FD Specific leaf area	0.01	-0.01	0.91
FD Seed mass	0.15	-0.01	0.70
FD Flowering time	0.01	-0.01	0.93

The MANOVA models analyzing variation along PC1 were all significant, except that for SLA (Table 3 and Fig. 3). Species richness decreased significantly with increasing intensification, although significant differences occurred only between the first and each of the other three intensification intervals (Tukey's HSD post-hoc test, p<

0.05). FD of plant height decreased significantly with intensification, although only the differences of intervals 1 and 2 with respect to intervals 3 and 4 were significant (Tukey's HDS post-hoc test, $p< 0.05$). FD of seed mass and flowering onset increased with intensification, but significant variation occurred only in intervals 1 and 2 in relation to intervals 3 and 4 (Tukey's HDS post-hoc test, $p< 0.05$ in both cases). There were no significant differences between intensification levels as to FD of SLA. In summary, intensification at field level resulted in ΔDSF vectors describing a non-linear pattern of decreasing functional redundancy along the intensification gradient (Fig. 3).

Table 3. Results of MANOVA evaluating the variation between equal-length intervals of increasing field level intensification (PC1) in sampled field Species Richness and Functional Diversity (FD) of the four traits considered. Results for Species Richness were the same in all models.

	$F_{3,74}$	Adjusted R^2	P
Species Richness	3.86	0.10	< 0.05
FD Height	6.02	0.16	< 0.001
FD Specific Leaf Area	0.90	0.00	0.44
FD Seed mass	5.76	0.16	< 0.01
FD Flowering onset	11.96	0.30	< 0.001

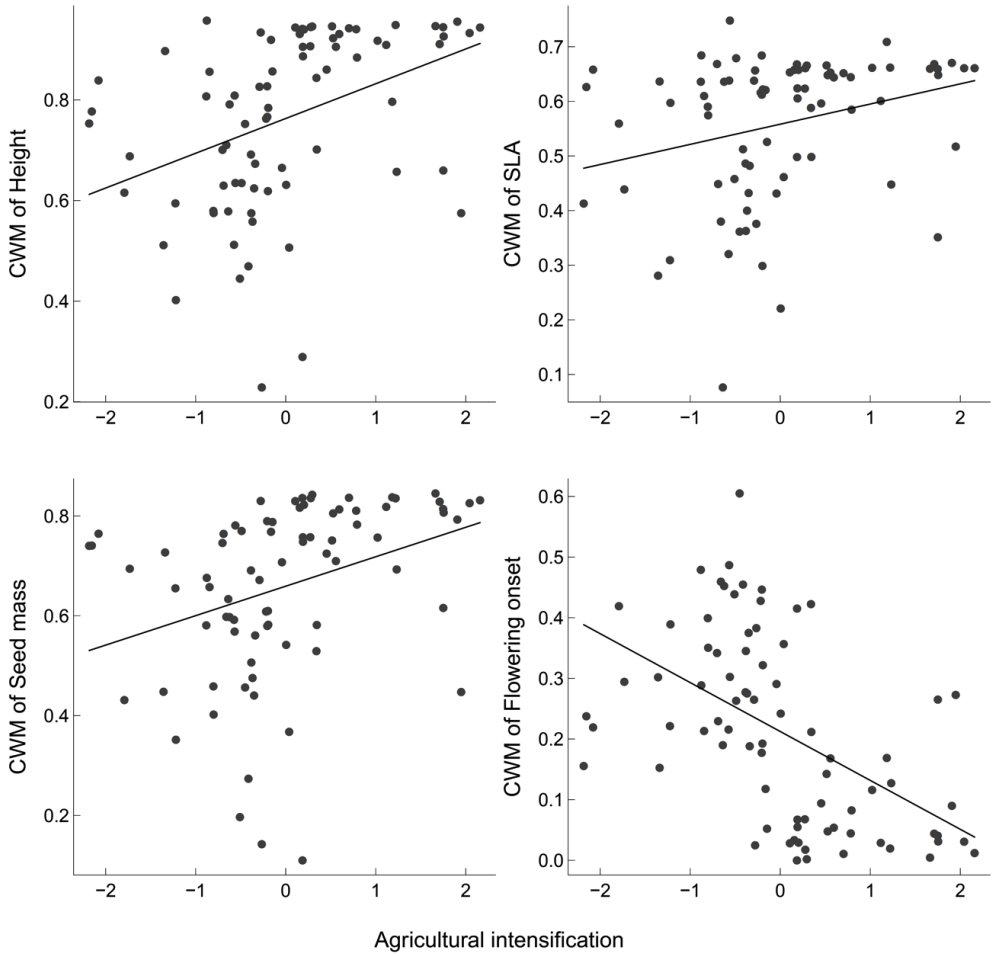

Fig. 1. Relationship between agricultural intensification at field level and Community Weighted Mean (CWM) values for different traits of arable plants: (a) Height ($F_{1,76}$ = 14.13 , adjusted R^2 = 0.15, P < 0.001); (b) SLA ($F_{1,76}$ = 6.30 , adjusted R^2 = 0.06, P < 0.05); (c) Seed mass ($F_{1,76}$ = 9.70 , adjusted R^2 = 0.10, P < 0.01); (d) Flowering onset ($F_{1,76}$ = 27.87, adjusted R^2 = 0.26, P < 0.001).

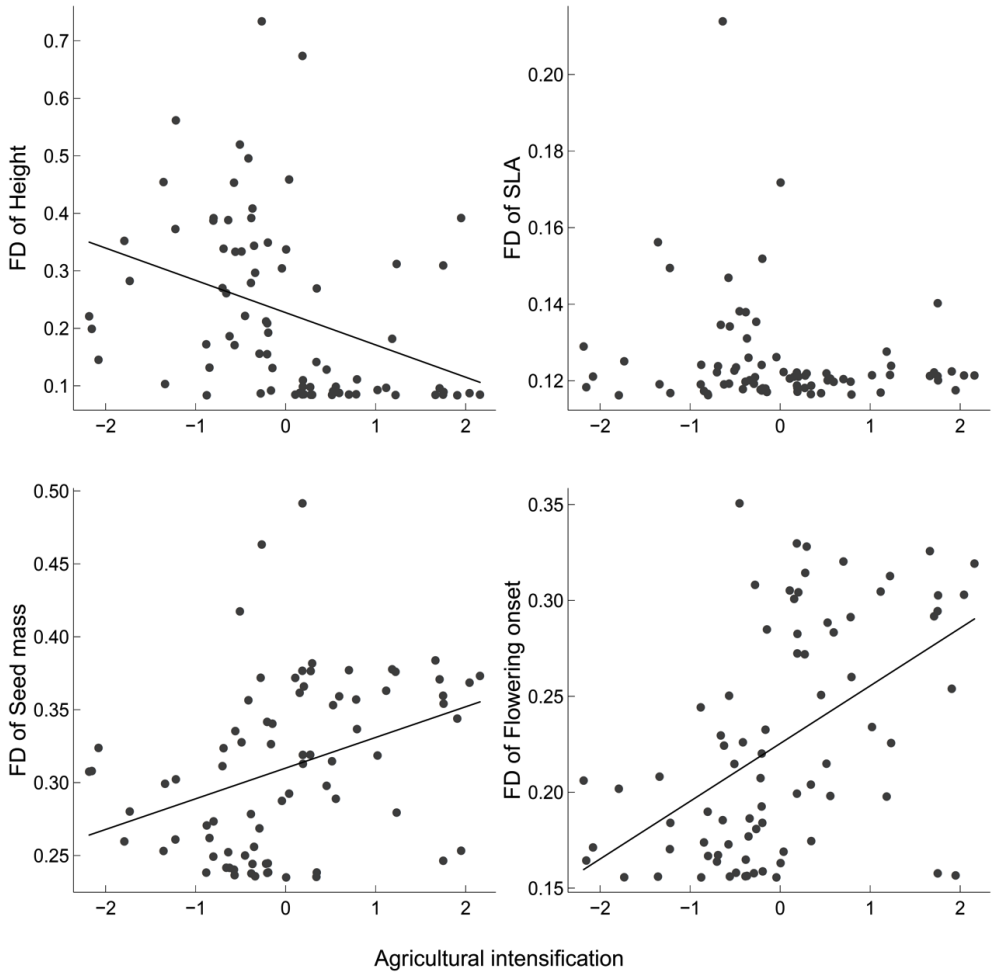

Fig. 2. Relationship between agricultural intensification at field level and Functional Diversity (FD) values for different traits of arable plants: (a) Height *($F_{1,76}$* = 11.67 , adjusted R^2 = 0.12, $P < 0.01$); (b) SLA ($F_{1,76}$ = 1.75 , adjusted R^2 = 0.01, P = 0.19); (c) Seed mass ($F_{1,76}$ = 11.35, adjusted R^2 = 0.12, $P < 0.01$); (d) Flowering onset ($F_{1,76}$ = 26.07, adjusted R^2 = 0.25, $P <$ 0.001).

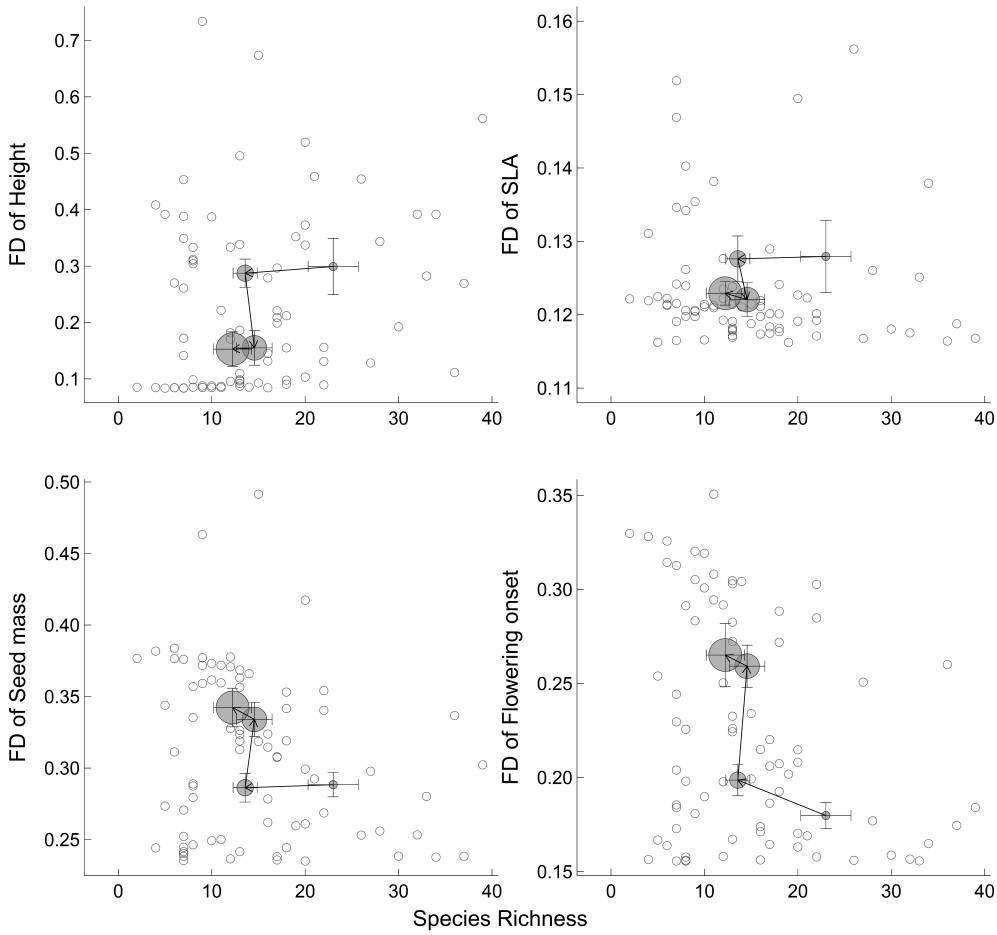

Fig. 3. Relationship between species richness and Functional Diversity (FD) values for different traits of arable plants (a) Height ($F_{1,76}$ = 1.75 , adjusted R^2 = 0.03, P = 0.07); (b) SLA ($F_{1,76}$ = 0.78, adjusted R^2 = -0.003, P = 0.38); (c) Seed mass ($F_{1,76}$ = 4.35, adjusted R^2 = 0.04, P < 0.05); (d) Flowering onset ($F_{1,76}$ = 7.88, adjusted R^2 = 0.08, P < 0.01). Shaded circles represent the mean values of FD and Species Richness for the corresponding four equal-length intervals along the field level intensification gradient (PC1; smallest: lowest intensification; largest: highest intensification). Error bars indicate ± SE. Arrows indicate the trajectories of change in species richness and FD of each trait (ΔDSF vectors) in relation to agricultural intensification.

Discussion

Our objective was to examine the relationship between arable plant species richness and functional diversity along intensification gradients at field and landscape levels in an arable agro-ecosystem. The influence of intensification at the landscape level on the functional diversity of arable plant flora was much smaller than that of management practices developed at field level. Besides, we found that increased levels of intensification at the field level selected for trait values that indicate a shift towards faster resource-use strategies, an observation consistent with our first prediction. The relationship between FD of the different traits and species richness revealed that the studied communities presented a great number of functionally redundant species. However, we found that this relationship varied significantly along the intensification gradient, a feature that can have potential implications for the management of these systems.

Field level versus landscape intensification effects on arable plant functional diversity

The landscape structure has been found to be important for biodiversity conservation in agricultural fields (e.g. Tscharntke *et al*. 2005), but its relative importance depends on the taxonomical group considered (Guerrero *et al*. 2010). Indeed, we did not find significant correlations between intensification at the landscape level and the analyzed traits. The lack of influence of the surrounding landscape in this study, in which we have avoided the field edges, may be attributed to the higher agricultural pressure towards the center of fields compared to the edges and to the lower probability of seed arrival because of the distance to field margins (Marshall 1989). This result is

consistent with other studies considering inner areas of fields in Mediterranean farmland (Romero, Chamorro & Sans 2008; José-María *et al.* 2011), suggesting that arable plant conservation policies in Mediterranean cereal fields should focus on farming practices (Armengot *et al.* 2011).

Arable plant functional trait composition

Our results showed that management intensification at field level results in arable plant communities with heavier seeds, higher SLA, higher canopies and earlier flowering. This combination of traits confers species the capacity to persist in the highly productive environments dominated by the crop species. Early flowering has been interpreted as a strategy to avoid competition (Franklin 2008). Tall species have a better access to light than short ones (Grime 2001). Species with high SLA show high relative growth rate and productivity (Westoby, Leishman & Lord 1996), being better adapted to resource-rich environments (Ordóñez *et al.* 2009), like the intensified fields with a high supply of fertilizers. Finally, seedlings of heavier-seeded species are better able to survive hazards including deep shade, physical damage and the presence of competing crop vegetation (Westoby, Leishman & Lord 1996). However, a typical weedy trait, like high seed output (e.g. Sutherland 2004) is associated to small seeds as predicted by life history trade-off theory (Charnov 2002; Ben-Hur 2012). In our case, apparently, the advantages gained by having larger seeds exceed those provided by the improved colonizing capacity conferred by a high seed output. Altogether, these results suggest that agricultural intensification produces a shift from relatively slower resource-use strategies towards a more rapid

consumption of resources, reflecting a trade-off between nutrient conservation and fast growth, thus supporting our first prediction. Intensive management practices would allow species in the most productive end of the gradient a faster use of nutrients and growth, but for shorter times (Pakeman, Lennon & Brooker 2011; Mason *et al.* 2012), emphasizing the idea that agricultural intensification reinforces the "weedy character" of arable plant species.

Functional diversity and intensification in arable plant communities

Only FD of plant height adjusted to our prediction of reduced functional diversity at high intensification levels. FD of seed mass and FD of flowering onset increased with intensification, while SLA showed no significant relationship. In accordance to this, Pakeman, Lennon & Brooker (2011) did not find consistent patterns of trait diversity change in relation to ecosystem productivity. The most common pattern across the 12 traits tested by these authors was for a decreased FD with increased productivity, which would indicate reduced variance in traits and trait convergence (oppositely, increased FD would imply higher variance in traits and thus trait divergence). Applying this reasoning to our results, agricultural intensification would be associated with trait convergence for plant height and with trait divergence for seed mass and flowering onset.

Intensification was also related with higher CWM for plant height and seed mass and with lower CWM for flowering onset. Both trends suggest that intensification causes a loss of smaller species and the incorporation of heavy seeded and early flowering ones, which is

consistent with the expected decrease in light availability in the most intensified fields with higher crop density.

Patterns of functional diversity vs. species richness in relation to intensification

In accordance with previous works, intensification reduced species richness (Fig. 3; Gabriel, Thies & Tscharntke 2005; Guerrero *et al.* 2010; Armengot *et al.* 2011; Storkey *et al.* 2012). However, this reduction was not associated with a reduction in FD for some of the studied traits, but rather with an increase in the FD of seed mass and flowering onset (Fig. 2), which is not in agreement with previous studies (eg. Flynn *et al.* 2009). One possible explanation could be that agricultural intensification, besides reducing species richness, induces changes in environmental filters, favoring the invasion of novel functional types for these traits (Mayfield *et al.* 2010). Nevertheless, we found a negative relationship between intensification and the FD of plant height and no relation for the FD of SLA. This result concurs with the notion that different niche axes can be differently affected by increases in resource availability (Spasojevic & Suding 2012).

The simultaneous examination of variation of species richness and FD in relation to intensification showed that the larger loss of species occurred between the first and second increasing intensification intervals. However, FD did not change significantly until intensification continued to increase (Fig. 3; second to third intervals), with lower diversity of vegetative traits, like plant height and higher diversity of reproductive ones, like seed mass and flowering onset. This decoupling between vegetative growth and reproduction in response to agricultural management is consistent with the empirical

evidence revised by Grime (2006). Environmental filters related to ecosystem productivity induce convergence in vegetative traits (implicated in dry matter production, carbon storage, etc.), while filters related to disturbance generate divergence in regenerative and phenological traits. In the case of arable plants in agro-ecosystems, both types of environmental filters would be governed (at least in part) by field management practices. In our study area, the amount of fertilizer is correlated not only with productivity, but also with disturbance, since higher amounts of fertilizer are associated with a higher frequency of applications.

At the highest extreme of the intensification gradient (Fig 3; third to fourth intervals), neither species richness nor FD changed significantly, which suggests a certain resistance of these arable plant communities to management intensification. This result would imply that in these communities, remnant species and functional groups are characterized by intensification-resistant traits.

In summary, the trajectories of change in species richness and FD of each trait (ΔDSF vectors, Mayfield *et al.* 2010) point at a non-linear pattern of decreasing functional redundancy along the intensification gradient. To our knowledge, this pattern has not been previously described in arable plant communities (but see Sasaki *et al.* 2009 for a similar one along a grazing gradient in grassland plant communities). Redundant species are considered necessary to ensure ecosystem resilience to disturbance (Walker 1992). Given the key roles played by arable plants in agro-ecosystems, the identified pattern has important implications for the consequences of management intensification on the functioning of these systems. The detected abrupt loss of

functional redundancy as intensification increases suggests the existence of ecological thresholds and probable sudden shifts from desired to less desired states in their capacity to generate ecosystem services (Folke *et al.* 2004). The combined and often synergistic effects of natural and man-made pressures can make agro-ecosystems more vulnerable to changes that were previously more easily buffered, which might be critical for system functioning and sustainable use of ecosystem services (Hooper *et al.* 2005).

Our results add to those of previous studies that have underscored the importance of considering species and functional diversities simultaneously in the study of ecosystem response to intensification (eg. Mayfield *et al.* 2010; Peco *et al.* 2012; Carmona *et al.* 2012). Moreover, by selecting the same index of functional diversity as some of these studies (Mayfield *et al.* 2010; Peco *et al.* 2012), we have ensured that our results are directly comparable with theirs (Mouchet *et al.* 2010).

Conclusions

Our study provides new insights on how agricultural management interacts with plant community structure and functioning through its non-linear effects on functional redundancy. The response of the considered functional traits is primarily driven by intensification of farming practices at the field level, with a non-significant effect of the surrounding landscape context. In line with our predictions, as intensification increases a shift towards fast resource-use strategies takes place in the functional trait composition of the arable plant community. However, trait diversity did not decrease with intensification, as we expected. In fact, diversity of reproductive traits

like seed mass and flowering onset increased, probably due to invasion by species better adapted to the conditions found in the more intensified fields. At the first stages, intensification caused a loss of redundant species, as indicated by the lack of changes in FD. Subsequent increases in intensification caused dramatic changes in the FD of the affected communities, but with opposed outcomes for vegetative and regenerative traits. Further increases in intensification resulted only in a small additional loss of species, suggesting that species in these communities are highly adapted to the conditions imposed by intensification, but with no change in FD, indicating again a high functional redundancy at these later stages.

In order to enhance our ability to preserve arable plant biodiversity, associated services and system resilience, non-linear responses of agricultural communities, like the ones presented in this study, should be taken into consideration when designing and adopting appropriate management strategies.

Acknowledgements

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Supporting Information

Table S1. List of sampled species with their corresponding family and assigned values of the functional traits considered. Blanks indicate missing data. Percentages represent the average proportion of cover of species with known trait values for each trait.

Species	Family	Height 98.38%	SLA 85.97%	Seed mass 99.96%	Flowering onset 96.38%
Aegilops triuncialis	Poaceae	0.40		12.35	6.0
Agrostis pourretii	Poaceae	0.11	26.20	0.11	5.5
Alopecurus myosuroides	Poaceae	0.30	27.27	2.15	
Anacyclus clavatus	Asteraceae			0.50	4.0
Anagallis arvensis	Primulaceae	0.13	29.22	0.49	4.5
Anchusa azurea	Boraginaceae	0.89	19.04	11.10	5.5
Andryala integrifolia	Asteraceae	0.28	24.12	0.19	7.5
Anthemis arvensis	Asteraceae	0.27	45.19	0.76	4.5
Aphanes arvensis	Rosaceae	0.09	17.70	0.22	
Avena sterilis	Poaceae	0.27	33.18	59.23	4.5
Bellardia trixago	Scrophulariaceae	0.19	19.28	0.04	4.5
Bromus diandrus	Poaceae	0.20		8.44	4.0
Bromus hordeaceus	Poaceae	0.17	12.77	1.45	4.5
Bromus madritensis	Poaceae	0.18	39.75	2.56	4.0
Bromus rubens	Poaceae	0.20		1.67	4.5
Bromus sterilis	Poaceae	0.38	33.67	7.49	4.5
Bromus tectorum	Poaceae	0.38	34.79	3.05	4.0
Buglossoides arvensis	Boraginaceae	0.35		6.28	4.0
Bupleurum rotundifolium	Apiaceae	0.30	28.73	3.33	4.5
Campanula erinus	Campanulaceae	0.20			4.0
Campanula rapunculus	Campanulaceae	0.50	44.42	0.03	5.0
Capsella bursa-pastoris	Cruciferae	0.13	27.92	0.10	8.5
Carduus tenuiflorus	Asteraceae	0.45		3.23	4.5
Carthamus lanatus	Asteraceae	0.40		10.39	7.0
Caucalis platycarpos	Apiaceae	0.18		19.59	
Centaurea cyanus	Asteraceae	0.72	21.06	6.18	
Centaurea melitensis	Asteraceae	0.40		1.39	6.0
Cerastium glomeratum	Caryophyllaceae	0.15	20.74	0.05	3.5
Chamaemelum mixtum	Asteraceae	0.25	25.44	0.14	6.5
Chenopodium album	Chenopodiaceae	0.48	22.21	0.65	8.0

Chondrilla juncea	Asteraceae	0.50	6.49	0.67	7.0
Cirsium vulgare	Asteraceae	0.90	14.70	2.48	6.5
Cnicus benedictus	Asteraceae	0.39	31.41	29.89	4.5
Convolvulus arvensis	Convolvulaceae	0.80	26.17	0.35	6.5
Conyza canadensis	Asteraceae	0.53	22.41	0.05	6.5
Coronilla scorpioides	Leguminosae	0.20			5.0
Corynephorus divaricatus	Poaceae				5.0
Crepis biennis	Asteraceae	0.58	31.23	1.31	
Crepis capillaris	Asteraceae	0.28	28.07	0.22	4.5
Echium plantagineum	Boraginaceae	0.30	32.85	2.97	4.0
Erysimum repandum	Cruciferae	0.15		0.24	
Euphorbia serrata	Euphorbiaceae	0.40		7.60	3.5
Filago pyramidata	Asteraceae	0.13	32.40	0.05	5.5
Filago vulgaris	Asteraceae	0.25	27.30	0.05	
Galium murale	Rubiaceae	0.20		0.18	4.5
Galium tricornutum	Rubiaceae	0.60	23.09	8.45	4.5
Geranium molle	Geraniaceae	0.18	27.63	1.09	4.0
Hordeum murinum	Poaceae	0.37	33.44	9.27	3.5
Hordeum vulgare	Poaceae	0.94	26.36	40.91	
Hypochaeris glabra	Asteraceae	0.17	39.45	0.62	3.5
Juncus bufonius	Juncaceae	0.06	17.87	0.03	5.5
Lactuca serriola	Asteraceae	0.68	16.59	0.54	7.5
Lamium amplexicaule	Lamiaceae	0.13	19.70	0.58	3.5
Lathyrus angulatus	Leguminosae	0.13	26.27	6.65	3.5
Leontodon taraxacoides	Asteraceae	0.05	17.40	0.80	4.5
Linaria spartea	Scrophulariaceae	0.55	10.00	0.02	4.5
Linum strictum	Linaceae	0.20		0.32	5.5
Logfia gallica	Asteraceae	0.05	28.49	0.02	5.5
Lolium rigidum	Poaceae	0.53	25.30	3.80	5.5
Lotus conimbricensis	Leguminosae			0.55	5.0
Lupinus angustifolius	Leguminosae	0.15	13.02	165.00	3.5
Mantisalca salmantica	Asteraceae				8.5
Medicago orbicularis	Leguminosae	0.40		3.80	5.0
Melilotus indica	Leguminosae	0.30	20.60	2.24	4.5
Ornithopus compressus	Leguminosae	0.10	25.06	2.47	4.0
Papaver rhoeas	Papaveraceae	0.36	33.07	0.11	4.0
Parentucellia latifolia	Scrophulariaceae	0.11	28.61	0.02	4.0
Picnomon acarna	Asteraceae			11.32	8.0
Plantago coronopus	Plantaginaceae	0.04	19.62	0.17	4.0

Plantago lagopus	Plantaginaceae	0.04	18.83	0.39	4.0
Polycarpon tetraphyllum	Caryophyllaceae	0.17		0.03	5.5
Polygonum aviculare	Polygonaceae	1.14	28.88	1.82	6.0
Polypogon monspeliensis	Poaceae			0.14	5.5
Ranunculus arvensis	Ranunculaceae	0.31	27.40	12.61	4.0
Ranunculus trilobus	Ranunculaceae	0.02	22.00	0.30	4.0
Raphanus raphanistrum	Cruciferae	0.35	25.63	26.24	4.5
Rapistrum rugosum	Cruciferae	0.51	23.00	3.13	
Reseda luteola	Resedaceae	0.70	21.09	0.29	5.0
Rumex pulcher	Polygonaceae	0.25		2.27	5.5
Senecio vulgaris	Asteraceae	0.20	29.82	0.27	3.5
Silene gallica	Caryophyllaceae	0.32	34.50	0.33	6.0
Silene muscipula	Caryophyllaceae				5.5
Silybum marianum	Asteraceae	0.85		22.75	4.5
Sonchus asper	Asteraceae	0.48	24.97	0.28	6.5
Sonchus oleraceus	Asteraceae	1.08	40.42	0.33	6.5
Spergularia rubra	Caryophyllaceae	0.11	18.30	0.03	4.5
Stellaria media	Caryophyllaceae	0.14	53.68	0.39	9.0
Taeniatherum caput-medusae	Poaceae			2.67	4.5
Tolpis barbata	Asteraceae	0.10	25.91	0.10	6.0
Tragopogon dubius	Asteraceae	0.43	25.52	8.24	
Trifolium angustifolium	Leguminosae	0.11	17.63	1.28	5.5
Trifolium arvense	Leguminosae	0.15	18.72	0.33	5.0
Trifolium campestre	Leguminosae	0.29	27.08	0.32	7.0
Trifolium glomeratum	Leguminosae	0.07	31.87	0.45	4.5
Trifolium lappaceum	Leguminosae			0.90	5.5
Trifolium resupinatum	Leguminosae	0.10	34.55	0.68	5.5
Trifolium tomentosum	Leguminosae	0.04	20.10	0.51	5.0
Trisetum paniceum	Poaceae			0.05	6.5
Veronica hederifolia	Scrophulariaceae	0.19	45.88	4.16	3.5
Vicia lathyroides	Leguminosae	0.10	25.80	2.30	5.0
Vicia lutea	Leguminosae	0.28		28.60	4.0
Vicia sativa	Leguminosae	0.55	22.86	31.05	4.5
Vulpia ciliata	Poaceae	0.14	13.50	0.12	5.0
Vulpia muralis	Poaceae	0.11	15.15	0.10	
Vulpia myuros	Poaceae	0.20	22.38	0.42	4.5

Table S2. Soil attributes of the sampled agricultural fields. Soil types according to IUSS Working Group WRB (2007): Cmca (Calcaric Cambisol), FLca (Calcaric Fluvisol) , LVcc (Calcaric Luvisol), LVvr (Vertic Luvisol), RGdy (Dystrict Regosol). Textural classes: Coarse (clay < 18 % and sand > 65 %), Medium (18% < clay < 35% and sand > 15%, or clay < 18% and 15% < sand < 65%). Textural class and parent material according to European Commission (2006). Agricultural intensification category: the four equal-length intervals of increasing field-level intensification along PC1 (see main text).

Field ID	Terrain %slope (mean±SD)	Soil type	Textural class	Parent material	Agricultural intensification category
1	1.12±0.28	CMca	Medium	Unconsolidated deposits	1
2	1.17±0.23	CMca	Medium	Unconsolidated deposits	
3	2.69±0.27	CMca	Medium	Unconsolidated deposits	
4	1.68±0.14	CMca	Medium	Unconsolidated deposits	
5	1.37±0.1	FLca	Medium	Unconsolidated deposits	
6	1.71±1.65	FLca	Medium	Unconsolidated deposits	
7	10.58±4.85	CMca	Medium	Unconsolidated deposits	
8	1.41±0.61	CMca	Medium	Unconsolidated deposits	
9	4.51±2.02	CMca	Medium	Unconsolidated deposits	
10	1.7±0.12	CMca	Medium	Unconsolidated deposits	2
11	2.35±0.41	CMca	Medium	Unconsolidated deposits	
12	1.31±0.75	CMca	Medium	Unconsolidated deposits	
13	2.3±0.22	CMca	Medium	Unconsolidated deposits	
14	1.95±0.11	CMca	Medium	Unconsolidated deposits	
15	1.37±0.32	CMca	Medium	Unconsolidated deposits	
16	1.47±0.43	CMca	Medium	Unconsolidated deposits	
17	4.57±0.35	LVvr	Coarse	Consolidated sedimentary rocks	
18	4.75±0.55	LVvr	Coarse	Consolidated sedimentary rocks	
19	2.84±0.54	LVvr	Coarse	Consolidated sedimentary rocks	
20	0.82±0.02	FLca	Medium	Unconsolidated deposits	
21	0.87±0.03	FLca	Medium	Unconsolidated deposits	
22	1.06±0	FLca	Medium	Unconsolidated deposits	
23	1±0.02	FLca	Medium	Unconsolidated deposits	
24	1.42±0.15	CMca	Medium	Unconsolidated deposits	
25	1.87±0.24	CMca	Medium	Unconsolidated deposits	
26	2.51±0.12	CMca	Medium	Unconsolidated deposits	
27	2.27±0.26	CMca	Medium	Unconsolidated deposits	
28	2.28±0.07	FLca	Medium	Unconsolidated deposits	
29	1.7±0.1	FLca	Medium	Unconsolidated deposits	
30	1.17±0.04	FLca	Medium	Unconsolidated deposits	
31	1.87±0.08	CMca	Medium	Unconsolidated deposits	
32	1.84±0.66	CMca	Medium	Unconsolidated deposits	
33	2.85±0.35	CMca	Medium	Unconsolidated deposits	

34	3.45±0.58	CMca	Medium	Unconsolidated deposits	
35	2.53±0.56	CMca	Medium	Unconsolidated deposits	
36	3.48±0.51	CMca	Medium	Unconsolidated deposits	
37	4.24±0.22	CMca	Medium	Unconsolidated deposits	
38	3.39±1.62	CMca	Medium	Unconsolidated deposits	
39	5.93±3.27	CMca	Medium	Unconsolidated deposits	
40	8.67±5.81	CMca	Medium	Unconsolidated deposits	
41	4.87±3.3	CMca	Medium	Unconsolidated deposits	
42	3.28±2.05	CMca	Medium	Unconsolidated deposits	
43	1.5±0.34	CMca	Medium	Unconsolidated deposits	3
44	1.42±0.02	FLca	Medium	Unconsolidated deposits	
45	2±0.45	LVvr	Coarse	Consolidated sedimentary rocks	
46	7.52±2.42	RGdy	Medium	Metamorphic rocks	
47	3.11±0.43	RGdy	Medium	Metamorphic rocks	
48	3.27±0.68	RGdy	Medium	Metamorphic rocks	
49	5.06±3.03	RGdy	Medium	Metamorphic rocks	
50	9.34±2.17	CMca	Medium	Unconsolidated deposits	
51	3.8±0.39	CMca	Medium	Unconsolidated deposits	
52	2.44±0.42	LVvr	Coarse	Consolidated sedimentary rocks	
53	4.3±1.87	LVvr	Coarse	Consolidated sedimentary rocks	
54	6.78±2.73	CMca	Medium	Unconsolidated deposits	
55	6.91±2.77	CMca	Medium	Unconsolidated deposits	
56	2.86±0.71	FLca	Medium	Unconsolidated deposits	
57	4.46±2.33	LVcc	Medium	Unconsolidated deposits	
58	2.81±1.69	FLca	Medium	Unconsolidated deposits	
59	4.98±2.47	FLca	Medium	Unconsolidated deposits	
60	2.93±2.29	FLca	Medium	Unconsolidated deposits	
61	3.07±1.51	FLca	Medium	Unconsolidated deposits	
62	1.43±0.94	FLca	Medium	Unconsolidated deposits	
63	2.73±1.99	CMca	Medium	Unconsolidated deposits	
64	2.24±1.34	CMca	Medium	Unconsolidated deposits	
65	6.58±4.84	CMca	Medium	Unconsolidated deposits	
66	4.36±0.53	CMca	Medium	Unconsolidated deposits	4
67	5.03±0.47	CMca	Medium	Unconsolidated deposits	
68	5.64±0.63	CMca	Medium	Unconsolidated deposits	
69	2.82±0.78	FLca	Medium	Unconsolidated deposits	
70	2.73±0.77	FLca	Medium	Unconsolidated deposits	
71	2.81±0.36	FLca	Medium	Unconsolidated deposits	
72	1±0.21	FLca	Medium	Unconsolidated deposits	
73	1.11±0.14	FLca	Medium	Unconsolidated deposits	
74	0.96±0.05	FLca	Medium	Unconsolidated deposits	
75	4.14±3.59	LVvr	Coarse	Consolidated sedimentary rocks	
76	11.55±10.56	LVvr	Coarse	Consolidated sedimentary rocks	
77	3.17±1.12	LVvr	Coarse	Consolidated sedimentary rocks	
78	9.18±5.4	CMca	Medium	Unconsolidated deposits	

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DISCUSIÓN GENERAL

La producción agraria intensiva se considera una amenaza global para la biodiversidad (Donald et al. 2001). Esta amenaza es especialmente importante en Europa, donde las zonas agrarias representan la mayor extensión de hábitats para la vida silvestre, de forma que gran parte de la biodiversidad europea está contenida en estas áreas (Sanderson et al. 2005). Existe, por tanto, la necesidad de encontrar fórmulas de gestión agraria basadas en la búsqueda de una multifuncionalidad de los agro-ecosistemas, de modo que sean compatibles la producción agraria y la protección y promoción de la biodiversidad en el conjunto total del territorio (Pain y Dixon 1997). Sin embargo, a pesar de los importantes esfuerzos en las últimas dos décadas, en términos de medidas agroambientales y otras, los resultados no han sido siempre los esperados (Kleijn y Sutherland 2006, Batáry et al. 2010), persistiendo las tendencias negativas de las poblaciones de organismos ligadas a estos medios (Donald et al. 2006). En España, aunque el único estudio específicamente orientado a la evaluación de efectos de las medidas agroambientales a escala nacional (Carricondo et al. 2012) muestra algunos resultados positivos, la tendencia poblacional de las especies propias de medios agrarios sigue siendo negativa (SEO-BirdLife, 2012).

Con el fin de contribuir al desarrollo de medidas de conservación efectivas, el objetivo principal de esta Tesis ha sido analizar las relaciones entre los componentes de la intensificación agraria y la variación en la estructura y composición de las comunidades biológicas de los agro-ecosistemas cerealistas, tanto a nivel local (de campo de cultivo), como a nivel de los efectos agregados que las prácticas agrarias tienen en el paisaje.

En los Capítulos II y III, el análisis de estas relaciones entre factores de intensificación agraria y distintas características de las comunidades de aves ligadas a estos medios, se ha llevado a cabo a lo largo de un amplio gradiente geográfico, que cubre gran parte de Europa, de Norte a Sur y de Oeste a Este. Dada la amplitud de estos estudios, no es de extrañar que el componente geográfico haya mostrado una gran importancia a la hora de explicar la variabilidad en las características de estas comunidades. Así, por ejemplo, la localización de las zonas de estudio explica alrededor del 30 % de la variación en la abundancia de aves nidificantes en los campos censados (Figura 3 en Capítulo III) y un 57 % en el caso de la composición taxonómica (Figura 2 en Capítulo II). A pesar de la tendencia actual de la agricultura a homogeneizar los paisajes agrarios más allá de las diferencias regionales entre sistemas (Potter 1997), la importante fracción de variación explicada por las prácticas agrarias desarrolladas en cada zona de estudio (hasta el 17.5 % de la variación en la densidad de territorios y el 37.8 % de la variación en la composición de las comunidades de aves), indica la persistencia de notables diferencias entre los sistemas cerealistas de la Unión Europea. Estos sistemas muestran distintos grados de intensidad del uso del suelo, consecuencia de diferencias tanto climáticas, edafológicas y biogerográficas, como socio-económicas e históricas (Stoate et al. 2001), con efectos diferenciales en la estructura y composición de las comunidades de aves asociadas. Así pues, parecería apropiado el actual diseño general de la política agroambiental ligada a la PAC, con programas particularizados a nivel local en el diseño de sus medidas, siempre que se enfoquen a los

requerimientos ambientales específicos asociados a la agricultura de cada región europea en la que se apliquen (Kleijn y Sutherland 2003).

En relación con la conservación de las comunidades de aves, es oportuno destacar aquí los resultados obtenidos en el Capítulo II sobre las comunidades de aves esteparias en Europa. Se trata de comunidades muy singulares en cuanto a su composición en el contexto europeo (Suárez et al. 1997, Santos y Suárez 2005), integradas por especies objeto de importantes esfuerzos de conservación. De hecho, los programas agro-ambientales dirigidos a la conservación de este tipo de especies son los que muestran mayor superficie acogida en España (Oñate 2005). En principio, serían precisamente este tipo de programas, dirigidos en su objetivo y diseño a especies concretas, los que se consideran potencialmente más exitosos en sus resultados (Vikery et al 2004, Donald y Evans 2006). Sin embargo, mediante el análisis de la integridad de las comunidades de aves de medios agrarios a través de índices de diversidad funcional y distancia taxonómica, hemos encontrado que son las comunidades de Europa del Este las que presentan un mejor estado de conservación (Figura 1). En general las prácticas agrarias en estas regiones, más recientemente incorporadas a la Unión Europea, son menos intensivas y los declives experimentados por su biodiversidad parecen ser de menor magnitud (Donald et al. 2001). En España, y a pesar de algunos efectos positivos de los programas agro-ambientales sobre las comunidades de aves esteparias (Carricondo et al 2012), resulta preocupante que éstos no consigan frenar los efectos negativos de la intensificación sobre la integridad de las comunidades de aves de los sistemas cerealistas españoles (Morales et al. 2013).

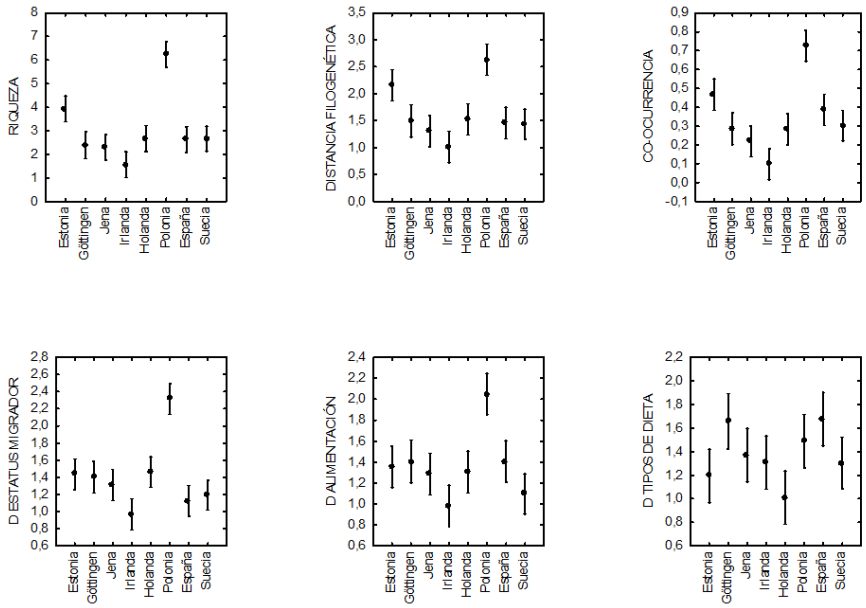


Figura 1. Diferencias entre ocho zonas de estudio europeas de los valores promedio de riqueza, distancia filogenética, probabilidad de co-ocurrencia y distintos índices de Simpson de diversidad funcional (estatus migratorio, estrategias de alimentación y tipos de dietas) de las comunidades de aves ligadas a los medios agrarios (ver detalles en Capítulo II). Las barras de error indican los intervalos de confianza al 95 % . (Morales et al. 2013).

Muy probablemente una de las dificultades a las que se enfrentan los esfuerzos de conservación de las comunidades biológicas en los paisajes agrarios radica en la diversidad, y en ocasiones la disparidad, de los requerimientos de los distintos grupos taxonómicos y especies objetivo (Suárez 2004), lo cual dificulta el diseño de medidas que consigan beneficiar de forma general a todos sus componentes (p.e. Gabriel et al. 2010, Concepción et al. 2012). En este contexto, a lo largo de esta Tesis, hemos presentado diversos análisis encaminados a identificar los efectos concretos de distintos factores de gestión de los sistemas cerealistas sobre estas comunidades (Capítulos I, II, III y IV).

Nuestros resultados corroboran esa diversidad de respuestas frente a los factores concretos de intensificación agraria. Así, en el Capítulo I, donde hemos analizado la respuesta de tres grupos taxonómicos distintos (aves, carábidos y plantas vasculares) a varios factores de intensificación en un sistema cerealista mediterráneo, ninguno de los once factores considerados consigue explicar simultáneamente las variaciones de riqueza específica de los tres grupos en estudio (Tabla 5 Capítulo I), en los que sus respectivas capacidades de dispersión producen respuestas que operan a distintas escalas espaciales. En el marco del propio proyecto AGRIPOPES en el cual se enmarca nuestro estudio, Geiger et al. 2010 encontraron diferencias similares en la respuesta de los mismos grupos en un estudio a escala continental.

Por otro lado, en los Capítulos II y IV, donde hemos analizado la relación entre la abundancia de distintas especies de aves y factores concretos de intensificación agraria, encontramos que las especies que componen estas comunidades responden a factores distintos en función de sus requerimientos específicos. Así, en el Capítulo II, el análisis de correspondencias canónicas (Figura 3b en Capítulo II) muestra, por ejemplo, que especies como la avutarda común (*Otis tarda*) y el aguilucho cenizo (*Circus pygargus*) aparecen asociados a paisajes dominados por el cultivo de cereal, mientras que otras, como el sisón común (*Tetrax tetrax*) y la cogujada común (*Galerida cristata*), responden a la variación de la riqueza taxonómica de plantas arvenses en los campos muestreados, es decir, variables de pequeña escala que pueden ser categorizadas como de microhábitat (en el caso concreto del sisón, esta relación es consistente con resultados monoespecíficos de selección de microhábitat; Faria et al. 2012). De forma similar, en el Capítulo IV en el que hemos analizado la

influencia de factores concretos de intensificación agraria sobre la abundancia de territorios de paseriformes asociados a los cultivos de cereal, los resultados indican que si bien el triguero (*Miliaria calandra*) depende de paisajes con un alto porcentaje de tierras cultivadas y campos de pequeño tamaño, la cogujada común (*Galerida cristata*) es sensible al rendimiento agrícola de los campos en los que nidifica (Figuras 3 y 4 en Capítulo IV). Es más, en el Capítulo III, observamos que dentro de una misma especie (la alondra común, *Alauda arvensis*), los requerimientos varían en función de la actividad que las aves desarrollan en el cultivo. Así, la importancia relativa de factores como la diversidad de usos del suelo en el paisaje agrario, el tamaño de campo o su rendimiento agrícola, cambia según se trate de individuos que simplemente se alimentan en dicho cultivo, o de individuos que nidifican en él, estableciendo un territorio reproductor (Figuras 4 y 5 en Capítulo III), con el consiguiente aumento de la demanda de recursos (tróficos, de refugio, etc.) por parte de las aves que utilizan dichos campos.

A la dificultad que plantea esta diversidad de requerimientos, se unen las interrelaciones entre factores individuales, que hacen de la intensificación agraria un complejo proceso multifactorial (Chamberlain et al. 2000), y las interacciones entre distintos grupos taxonómicos y niveles tróficos, como la influencia de las comunidades de plantas o invertebrados sobre las comunidades de aves (Capítulo II), e incluso las relaciones interespecíficas dentro de las propias comunidades (Capítulo IV).

Sin embargo, en términos generales, las comunidades estudiadas parecen responder a factores efectivamente relacionados, por un lado,

con el aumento de la apropiación humana de producción primaria a través de la cosecha, por medio de la mayor aportación de fertilizantes, pesticidas y dosis de simiente; y, por otro lado, con factores relacionados con la simplificación de los agro-ecosistemas, ligada al creciente tamaño de explotaciones y campos de cultivo y a la pérdida de diversidad de sustratos y hábitats en los paisajes estudiados. Estos cambios se han resumido en una pérdida de heterogeneidad ambiental extendida a distintas escalas, tanto espaciales como temporales, que dificulta que los agro-ecosistemas intensificados proporcionen los recursos necesarios para mantener la diversidad de requerimientos de las comunidades biológicas asociadas (Benton et al. 2003, Sanderson et al. 2005). En este sentido, resulta llamativa la relación variable de la diversidad de usos del suelo, o el porcentaje de superficie cultivada, con las comunidades estudiadas. En el Capítulo I, hemos visto cómo la diversidad de usos del suelo influye positivamente en la riqueza taxonómica de la comunidad de carábidos de los sistemas cerealistas estudiados, mientras que disminuye la riqueza de la comunidad de aves. Esta última respuesta negativa se repite al analizar la relación de la diversidad de usos del suelo con la estructura o composición de las comunidades de aves (Capítulos II y III). A la hora de interpretar estos resultados, es importante notar que la comunidad de carábidos estudiada comprende todas las especies encontradas en los campos muestreados, mientras que la comunidad de aves se limita a aquellas que podemos considerar especialistas en medios agrarios de cereal (Tabla 1 en Contexto de la Tesis y Metodología General). Es por tanto comprensible que para la comunidad de carábidos, en la que no se considera la especialización, la presencia de distintos tipos de hábitats en el paisaje sume especies a

la comunidad. En el caso de las aves, por el contrario, la diversidad de distintos tipos de usos o coberturas de suelo, supone tanto la reducción de la extensión del medio propiamente agrario al que están ligadas, como la aparición de hábitats desfavorables (Duelli 1997), lo que parece afectar negativamente a esta comunidad de especialistas. Pero si bien la heterogeneidad ambiental está ampliamente aceptada como un factor de síntesis a la hora de comprender las relaciones entre la intensificación agraria y las comunidades de organismos de estos medios (Benton et al. 2003), la heterogeneidad relevante para cada especie o grupo de especies puede no ser la misma dependiendo de sus requerimientos particulares (Farigh et al. 2011). Así, como hemos visto en el Capítulo III, la comunidad de aves especialistas de medios agrarios sí responde a la diversidad y heterogeneidad del paisaje, pero medida esta vez a escala de distintos sustratos agrícolas (Figura 4 en Capítulo III). En efecto, se observa una relación positiva de esta comunidad frente a una mayor diversidad de cultivos y un menor tamaño de las parcelas cultivadas. Esta respuesta podría ser relevante a la hora de diseñar medidas de conservación de la biodiversidad en los agro-ecosistemas, ya que la diversificación del paisaje en términos de sustratos productivos podría constituir una mejora de la estructura y composición de los paisajes agrarios evitando el habitual rechazo que producen en los agricultores las medidas que prescriben el cese de producción en parte de la superficie cultivada como medida de extensificación (Farhig et al. 2011).

En relación con la diversidad de coberturas y usos del suelo en los paisajes agrarios, cabe, además, hacer una reflexión acerca de la utilización de la riqueza o diversidad taxonómicas como indicadores del estado de la biodiversidad, que ha sido cuestionada en varias

ocasiones, al considerar que su estudio puede llevar a conclusiones engañosas (Filippi-Codaccioni et al. 2010). Flohre et al. 2011, analizando la riqueza especifica de aves obtenida en el proyecto en que se enmarca esta Tesis, sin distinguir especialistas, encuentran relaciones positivas entre la diversidad de usos del suelo y la diversidad taxonómica de aves en las mismas áreas de estudio. Esto podría llevar a considerar un aumento de la diversidad de coberturas como una medida positiva para conservar las comunidades de aves en estas zonas, pero podríamos encontrarnos ante un proceso de homogeneización (McKinney y Lockwood 1999) en el que generalistas se unen a la comunidad aumentando su diversidad taxonómica a pesar del efecto negativo que el aumento de usos del suelo parece tener sobre las comunidades de especialistas (Capítulos I, II y III). En consecuencia, parece importante tener en cuenta esta respuesta diferencial de las medidas de biodiversidad, considerando en todo caso qué representan, a la hora de elaborar conclusiones y recomendaciones dirigidas a la conservación. En el caso de los medios agrarios europeos que nos ocupan, que no sólo albergan poblaciones de especies en preocupante declive en comparación con especialistas de otros medios, sino comunidades tan peculiares como las de aves esteparias mediterráneas, un aumento general del número de especies, sin atender a su naturaleza, no parece ser lo más conveniente.

Otro de los objetivos de esta Tesis ha sido analizar por separado los efectos de los componentes de la intensificación agraria a escala local (de campo de cultivo) y de paisaje, con la intención de distinguir sus efectos sobre la biodiversidad. En los Capítulos I, II y IV, este análisis se llevó a cabo a través del estudio de las relaciones de factores de intensificación, a ambas escalas por separado, mientras que en los

Capítulos III y V se analizaron los efectos de ambos componentes de forma agregada, determinando la importancia relativa que tienen sobre las comunidades de aves y plantas ligadas a los sistemas agrarios.

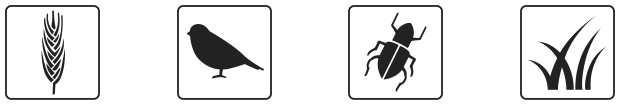
Tanto la estructura como la composición del paisaje alrededor de los campos de cultivo presentan efectos importantes sobre las comunidades estudiadas. Así, por ejemplo, hemos visto en el Capítulo I, cómo la diversidad de coberturas del suelo es el factor con mayor efecto sobre la riqueza específica de las comunidades de aves y carábidos en el sistema cerealista mediterráneo estudiado, y en el Capítulo III, hemos visto cómo la estructura y composición del paisaje explican, respectivamente, el 14 % y el 20 % de la variación de la densidad de individuos y territorios de aves especialistas a lo largo de un gradiente de intensificación europeo. Este componente paisajístico es considerado de gran importancia en las relaciones de la intensificación con las comunidades de especies en los sistemas agrarios, y se le otorga un papel determinante en la modulación de la efectividad de las medidas agro-ambientales sobre la biodiversidad (p.e. Tscharntke et al. 2005, Concepción et al. 2012). De hecho, una de las limitaciones que se plantean como causa de la falta de efectividad de muchas de estas medidas es su orientación exclusiva al campo de cultivo, sin considerar la estructura y composición del paisaje alrededor de los mismos (Wittingham 2007).

Si bien nuestros resultados confirman esta influencia del paisaje sobre las comunidades de especies de distintos grupos taxonómicos en los agro-ecosistemas europeos, también ponen de manifiesto la gran importancia que la gestión a nivel local, de cada campo de cultivo, tiene sobre estas comunidades. Así, en el Capítulo III, hemos visto

cómo las prácticas agrarias a nivel de parcela explican un 13 % de la variación de territorios de aves especialistas y un 18 % de territorios de alondra común (*Alauda arvensis*), superando en este caso la fracción de variación explicada por el componente de paisaje.

En esta línea de evidencia, es especialmente destacable la respuesta de las comunidades de plantas arvenses a los componentes de la intensificación agraria. En el Capítulo I, hemos visto cómo la composición del paisaje, a través de la densidad de lindes, medidas como tamaño medio de los campos en el paisaje alrededor de los puntos de muestreo, tiene un efecto positivo y significativo sobre la riqueza taxonómica de plantas arvenses. Por su parte, en el Capítulo V, se analizaron los efectos agregados, por un lado del componente local, y por otro, del paisajístico, separados mediante un análisis de componentes principales en dos ejes ortogonales. En este caso, se estudió la variación en la diversidad de cuatro rasgos funcionales en esta comunidad a lo largo de dos gradientes independientes de intensificación agraria: un gradiente de intensidad de uso del suelo a escala local, y un gradiente de estructura y composición a escala de paisaje. En este estudio, no encontramos correlaciones significativas entre la variación de diversidad de ninguno de los rasgos funcionales analizados y el gradiente de intensificación a escala de paisaje, pero sí comprobamos el importante efecto no lineal que las prácticas agrarias a nivel de campo de cultivo tienen sobre la composición funcional de estas comunidades, con una importante pérdida de especies con rasgos redundantes en los primeros estadios de intensificación, mientas que en niveles crecientes si bien continúa cambiando la diversidad funcional, deja de haber cambios en la riqueza de especies. Por tanto, sobre la base de los resultados de estos dos capítulos, podemos

concluir que la riqueza taxonómica y la diversidad funcional no responden de la misma forma al proceso de intensificación agraria. Consideramos estos resultados de gran relevancia, ya que la simplificación funcional de estas comunidades de plantas en los campos de cultivo repercute en el mantenimiento de otras comunidades biológicas (p.e. Marshall et al. 2003 y Capítulo II). De esta forma, los resultados obtenidos en el capítulo V parecen contradecir la idea de que los paisajes complejos (el porcentaje medio de superficie cultivada alrededor de los campos muestreados en la zona de estudio es 62.8 %, pudiéndose considerar cierta complejidad de paisaje) compensan el efecto negativo de la intensificación agraria a escala local en las comunidades de plantas arvenses (Weibull et al. 2003, Gabriel et al. 2005). En consecuencia, nos parece importante destacar que la simplificación paisajística asociada a la intensificación agraria ejerce una gran influencia sobre la biodiversidad de los sistemas agrarios europeos, y que el diseño de medidas de conservación dirigidas al mantenimiento de esta biodiversidad debería incluir mejoras a escala de paisaje para conseguir sus objetivos. Sin embargo, estas modificaciones no compensarían por sí solas el importante efecto negativo que las prácticas agrarias llevadas a cabo en los campos de cultivo tienen sobre las comunidades de organismos ligados a estos medios.



CONCLUSIONES

1. Los distintos factores de intensificación agraria, tanto a escala local, como de paisaje, afectan de forma diferencial a las comunidades biológicas de los medios agrarios. Estas diferencias de respuestas se dan tanto entre grupos de organismos en función de sus distintas capacidades dispersivas, como entre especies del mismo grupo taxonómico en función de sus distintos requerimientos específicos, o entre individuos de la misma especie con distintas necesidades fenológicas

2. La variabilidad en la composición taxonómica de las comunidades de aves ligadas a los medios cerealistas europeos se explica principalmente por el efecto de un doble gradiente geográfico/bioclimático y de intensificación agraria a escala europea. La asociación entre geografía y gestión aconseja un diseño de las medidas dirigidas a conservar las comunidades de aves de estos sistemas adaptado a los diferentes contextos agrarios.

3. El proceso de intensificación agraria afecta negativamente a la abundancia, la composición taxonómica y la diversidad funcional de las comunidades de aves especialistas de estos medios.

4. Las comunidades de aves especialistas se ven afectadas por la cantidad y calidad de hábitat agrario *per se*, siendo especialmente relevantes la composición y estructura del paisaje medido en términos de usos productivos. A través de modificaciones de la estructura del hábitat y de efectos sobre otros grupos taxonómicos que son sus recursos tróficos, a nivel local la intensificación agraria influye negativamente en estas comunidades, afectando especialmente a los individuos reproductores.

5. La gestión agraria llevada a cabo a nivel de parcela influye de manera particularmente importante en la biodiversidad asociada a la reproducción en cada parcela. Por tanto, sin olvidar los efectos de gestión a escala de paisaje, la extensificación de la gestión a nivel de parcela parece fundamental para asegurar la persistencia poblacional de las especies presentes.

6. El proceso de intensificación agraria afecta, principalmente actuando a escala local, a la riqueza taxonómica y a la diversidad funcional de las comunidades de plantas arvenses en sistemas cerealistas mediterráneos, si bien de forma diferencial.

7. La relación entre el grado de intensidad de las prácticas agrarias a escala local y las comunidades de plantas arvenses en sistemas cerealistas mediterráneos no es lineal, produciéndose los cambios más importantes de composición taxonómica y funcional en los primeros tramos del gradiente de intensificación.

8. La influencia de una mayor heterogeneidad en el agro-ecosistema a escala paisajística no siempre compensa los importantes efectos de la intensificación de las prácticas agrarias a nivel local sobre las comunidades de plantas arvenses en sistemas cerealistas mediterráneos.

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